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Nitrogen regulation by natural systems in "unnatural" landscapes: denitrification in ultra-urban coastal ecosystems

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ABSTRACT

Dense cities represent biogeochemical hot spots along the shoreline, concentrating fixed nitrogen that is subsequently discharged into adjacent coastal receiving waters. Thus, the ecosystem services provided by natural systems in highly urban environments can play a particularly important role in the global nitrogen cycle. In this paper, we review the recent literature on nitrogen regulation by temperate coastal ecosystems, with a focus on how the distinct physical and biogeochemical features of the urban landscape can affect the provision of this ecosystem service. We use Jamaica Bay, an ultra-urbanized coastal lagoon in the United States of America, as a demonstrative case study. Based on simple areal and tidal-based calculations, the natural systems of Jamaica Bay remove ~ 24% of the reactive nitrogen discharged by wastewater treatment plants. However, this estimate does not represent the dynamic nature of urban nitrogen cycling represented in the recent literature and highlights key research needs and opportunities. Our review reveals that ecosystem-facilitated denitrification may be significant in even the most densely urbanized coastal landscapes, but critical uncertainties currently limit incorporation of this ecosystem service in environmental management.

ARTICLE HISTORY

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KEYWORDS Nitrogen; denitrification; urban; coastal; anammox; wetlands

Introduction

Human activities have doubled the annual fixation of reactive nitrogen (Nr, Fowler et al. 2013), with global implications for human health, air and water quality, and biodiversity (Erisman et al. 2013). As a result, the development of strategies for effective nitrogen management remains a global priority, which must be considered concurrently with other aspects of global environmental change, such as urbanization. As global coastlines become increasingly urban (Blackburn and Marques 2014; von Glasow et al. 2013; McGranahan, Balk, and Anderson 2007), it remains unclear how, or, if coastal ecosystems will continue to provide nitrogen regulation services, and limited information is available to inform management in support of these ecosystem services. In this paper, we review the current literature on the nitrogen regulation role of temperate coastal ecosystems in highly urbanized areas. We use Jamaica Bay, an ultra-urbanized coastal lagoon in the USA, as a demonstrative case study to highlight key research needs and opportunities to support the management of these distinct environments.

Coastal ecosystems are known to be important control points in the global nitrogen cycle (Valiela, Teal, and Sass 1973; Jordan, Stoffer, and Nestlerode 2011). Located at the interface between land and sea, these systems contain a mosaic of interdependent habitats (Figure 1) that facilitate the transformation of N_r to dinitrogen gas (N₂) through microbial-mediated denitrification and anaerobic ammonium oxidation (Smyth et al. 2013; Damashek and Francis 2018). Since N₂ cannot drive primary production without thermodynamically costly "fixation" to Nr, denitrification and anammox are critical regulators of the nitrogen (N) cycle. The N-regulation services provided by coastal habitats play a key role in both moderating eutrophication and preventing anthropogenic Nr from being transported from terrestrial sources to the open ocean (Asmala et al. 2017; Bouwman et al. 2013; Teixeira et al. 2014).

Many studies, however, have demonstrated that eutrophication resulting from excessive N_r loading degrades coastal ecosystems and their ability to support nitrogen regulation (Hale 2016; Cornwell, Michael Kemp, and Kana 1999). Although denitrification rates generally increase with N_r loading, this relationship may be asymptotic at the landscape-scale, with a site-

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Figure 1. Examples of habitat found in temperate coastal ecosystems (a) Salt marsh islands, (b) Perimeter marsh downstream of a Combined Sewer Outfall, and (c) perimeter tidal creek and marsh platform. Images from Jamaica Bay, New York in 2011. Source: Bernice Rosenzweig.

specific saturation threshold beyond which coastal ecosystems can no longer continue to effectively regulate N_r (Drake et al. 2009; Yin et al. 2015; Eyre and Ferguson 2009). Coastal ecosystems are primarily N-limited and high loads of anthropogenic Nr can result in increased turbidity and hypoxia (de Jonge, Elliott, and Orive 2002; R. W. Howarth and Marino 2006), with potential feedbacks that reduce benthic denitrification or efficiency (Howarth et al. 2011). In highly eutrophic systems, there can also be a direct loss of the habitats that support the highest denitrification rates, as vascular vegetation is replaced by opportunistic macroalgae and where salt marsh becomes destabilized and erodes away (Deegan et al. 2012; Burkholder, Tomasko, and Touchette 2007; Howarth and Marino 2006; Cornwell, Michael Kemp, and Kana 1999).

Some of the highest N_r loading rates occur downstream of dense cities (Powley et al. 2016; Driscoll et al. 2003; Morée et al. 2013), where large quantities of nitrogen are imported as food to support concentrated populations and then discharged as wastewater (Kennedy et al. 2015; Powley et al. 2016; Luo et al. 2014). Many cities also concentrate nitrogen emitting vehicles and industrial facilities, which further contribute to local discharges of N_r to receiving waters (Huang et al. 2015). As a result, cities have been identified as global "hot spots" of N_r and, with continued megacity development, may serve as important control points in the global nitrogen cycle (Bernhardt et al. 2008; Newton, Carruthers, and Icely 2012). The circumstances and challenges of ecosystem N_r regulation in highly urbanized coastal zones are complex and unique within the global N cascade (Galloway et al. 2003).

Urbanization and coastal ecosystems

The N pathways of cities are often dominated by sewer systems that transport upland-generated N_r directly into receiving waterways, often completely bypassing the key N_r removal zones of less-developed landscapes, such as the subsurface of riparian and fringing coastal wetlands (Groffman et al. 2003; Valiela and Cole 2002). Cities with more stringent environmental protection policies rely on wastewater treatment plants (WWTPs) to process municipal wastewater and/or stormwater before they are discharged to receiving waters. However, many global cities do not yet utilize WWTPs and N_r -rich wastewater is discharged, untreated to receiving waters (Mateo-Sagasta, Raschid-Sally, and Thebo 2015; Malik et al. 2015).

Even when WWTPs are present, their efficacy in regulating N_r is highly dependent on the treatment

technologies employed. Many contemporary urban WWTPs provide only "secondary" treatment, which uses aerobic bioreactors to reduce the biological oxygen demand of wastewater but provides limited reduction of the wastewater N_r load (Malik et al. 2015). An increasing number of WWTPs also provide "advanced" treatment to facilitate N_r-removal (Rodriguez-Garcia et al. 2014). These advanced treatment technologies can reduce wastewater Nr from its influent concentration of 20 - 70 mg N/L to less than 1 mg N/L (Carey and Migliaccio 2009). Fully advanced treatment in large cities, however, can cost billions of dollars (Paulsen, Featherstone, and Greene 2007) and their implementation may be delayed by sociopolitical barriers (Garrone et al. 2016). The challenges of wastewater N_r treatment are also amplified in cities with combined sewer outfall systems (CSOs), where untreated sewage can bypass the WWTP entirely during heavy rain events (Bernhardt et al. 2008), resulting in pulses of high Nr effluent discharged directly to adjacent waterways (Driscoll et al. 2003).

Coastal ecosystems downstream from urban areas are frequently hypereutrophic due to the heavy N loading from wastewater (Kroeze et al. 2013; Bricker et al. 2008). This impacts their ability to serve as nitrogen "filters." In addition, other features of the engineered urban landscape can impact the ability of coastal ecosystems to provide nitrogen regulation services. For example, conventional urban development is associated with paving over large fractions of watershed area and the burial of natural stream channels, which concentrates freshwater discharge to areas downstream of sewer outfalls (Walsh et al. 2005; Paul and Meyer 2001). This can result in spatial and temporal patterns of salinity and sediment delivery that are distinct from those of coastal ecosystems in agricultural or pristine areas, with implications for the structure and function of urban wetlands and benthic ecosystems (Lee et al. 2006; Faulkner 2004).

Urban stormwater runoff may also contain a variety of contaminants that can impact the sediment biogeochemistry and ecosystem function of downstream receiving waters (Sutherland et al. 2016). As a result and, along with active or historic industrial activity, the sediments of coastal waterways adjacent to cities often sink for organic pollutants and metals (Islam and Tanaka 2004; Dachs and Laurence 2010). Densely populated cities in particular may concentrate a variety of "emerging contaminants," such as pharmaceuticals and microplastics, which are subsequently released into coastal waterways through groundwater, CSOs and WWTP discharges (Rosi-Marshall and Royer 2012; Arpin-Pont et al. 2016; Cole et al. 2011). The impacts of these compounds on coastal ecosystem function and biogeochemical processing are only beginning to be investigated, but initial studies

have found that they may bioaccumulate and influence survival, growth and reproduction in a variety of marine organisms, with implications for coastal trophic structure and in turn, Nr regulation processes. (Table 1).

Urban development is also frequently associated with engineered changes to the morphometry of adjacent coastal waterbodies, including landfilling, beach replenishment, and sediment dredging to create navigation channels and "borrow pits" for sand supply, or to support contaminant removal (Gustavson et al. 2008; Xue, Hong, and Charles 2004; Trimmer et al. 2005). Infrastructure such as groins, jetties, and riprap are commonly employed to support shoreline stabilization, and a variety of levees, storm surge barriers and seawalls may be utilized for coastal flood regulation (Hill 2015). The combined impacts of these engineering practices may alter the tidal range and prism that, in turn, lead to changes in circulation, water residence time, sediment dynamics and submarine groundwater flow, with implications for nutrient fate and transport (Duck and Da Silva 2012; Teatini et al. 2017; Haghani et al. 2016; Nixon et al. 1996). For example, Deek et al. (2013) observed that the recent reductions in denitrification capacity of the Elbe Estuary far exceeded reductions in NO₃⁻ load, which they postulated could be attributed to cooccurring anthropogenic alteration of the hydrology and morphometry of the estuary.

Coastal wetlands, which are now known to be particularly important habitat for Nr removal (Jordan, Stoffer, and Nestlerode 2011; Smyth et al. 2013), are particularly impacted by urban coastal engineering practices. Historically, wetlands were viewed as having little socioeconomic value, and they were targeted for landfilling to support municipal waste disposal or "reclaimed" for urban development in many cities (Gedan, Silliman, and Bertness 2009). Davidson (2014) estimates that 46-50% of global coastal wetlands have been lost since the start of the eighteenth century due to a variety of anthropogenic stresses including urban reclamation. The remaining urban coastal wetlands are directly impacted by a variety of engineering practices, including ditching, runnelling, or open marsh water management for mosquito control (Figure 2; Hulsman, Dale, and Kay 1989; Lee et al. 2006; Elsey-Quirk and Adamowicz 2016) or disconnection from uplands by shoreline stabilization infrastructure (O'Meara, Thompson, and Piehler 2015).

More recently, there has been increased interest in the restoration of coastal wetlands as environmental managers and policymakers became more aware of the ecosystem services they provide (Gedan, Silliman, and Bertness 2009). Debate continues about whether these restored marshes are able to provide the full suite of ecosystem services generated by natural wetlands. It is likely that their N_r regulation effectiveness

Table 1. Environmental controls on denitrification and anammox.

| Environmental Control | Effects on denitrification and anammox |
|---|---|
| Labile organic carbon | Denitrification is heterotrophic and dependent on the availability of organic carbon (Velinsky et al. 2017; Marchant et al. 2016; Gardner and McCarthy 2009; Smyth et al. 2013; Piehler and Smyth 2011; Deek et al. 2013). When/where labile organic carbon is abundant, denitrifying microorganisms usually outcompete anammox microorganisms for NO₂⁻, since denitrifying microorganisms vastly outnumber anammox microorganisms and, under most conditions, denitrification will be thermodynamically favored. (Thamdrup and Dalsgaard 2002; Lam and Kuypers 2011; Engström et al. 2005) Under some conditions, anammox has been observed to be positively correlated with sediment organic carbon since sediments with abundant organic carbon can support high rates of NO₂⁻ production, which can support increased rates of anammox even though denitrification is thermodynamically favored and remains relatively marce impactant. (Trimmer, Nichelle, and Deflandra 2002) |
| Nitrate (NO ₃)/Nitrite (NO ₂) concentrations | Denitrification rates are dependent on the availability of NO₃⁻ and NO₂⁻ Trimmer et al. (2005) observed a biphasic relationship between anammox rates and NO₃⁻ concentrations, which they attributed to competition for NO₂⁻ when its supply through denitrification is limited and enhancement of anammox when NO₂⁻ is generated in abundance by denitrification. |
| Ammonium (NH4 ⁺)/Ammonia (NH3) concentration | In systems with high NH₄⁺ concentrations (such as those that receive effluent from WWTPs): Anammox can actually be thermodynamically favored over denitrification (Babbin and Ward 2013). The occurrence of anammox under high NH₄⁺ loading would also be highly dependent on pH, since anammox bacteria have been found to be inhibited by the build-up NH₃ (Jin et al. (2012) |
| Turbidity/light penetration | Sea grass stands are hotspots of denitrification (Velinsky et al. 2017; Marchant et al. 2016; Gardner and McCarthy 2009; Smyth et al. 2013; Piehler and Smyth 2011; Deek et al. 2013). Reduced light penetration can degrade sea grass productivity and areal coverage (Valiela 2015; Burkholder, Tomasko, and Touchette 2007). |
| Anoxic water column | Although denitrification and anammox require localized anoxia to be thermodynamically favorable, anoxic water column conditions can: Directly inhibit coupled nitrification-denitrification Result in the accumulation of sulfide in surficial sediments, which inhibits both coupled nitrification-denitrification and anammox (Joye and Hollibaugh 1995; Jensen et al. 2008; Sears et al. 2004; Thamdrup and Dalsgaard 2002) Indirectly reduce the system-level rate of denitrification and anammox by changing the composition of benthic faunal communities, favoring species that are less effective for bioturbation. |
| Trace pharmaceuticals | Broad spectrum antibiotics: Are known to inhibit the synthesis of the enzymes needed to facilitate denitrification by microorganisms (Tiedje, Simkins and Groffman 1989) May also inhibit existing denitrification enzyme activity in microbes (Pell et al. 1996; Brooks, Smith and Macalady 1992) In laboratory studies designed to replicate the coastal environment, residual antibiotics and other pharmaceuticals may decrease overall rates of denitrification while also resulting in increased emissions of N₂O (Hou et al. 2015a; Yin et al. 2017, Yin et al. 2016). |
| Other urban pollutants | Heavy metal contamination can actually enhance denitrification in some settings by selecting for contaminant-tolerant species with increased burrowing activity, which can facilitate the transport of NO₃ into sediment zones where denitrification is favorable (Banks et al. 2013). Some organic contaminants and microplastics reduce burrowing activity in marine macroinvertebrates, with potential implications for nutrient transport, redox zonation and the occurrence of denitrification and anammox (Green et al. 2016). |

varies with the broad variety of restoration techniques utilized (Meli et al. 2014; Mossman, Davy, and Grant 2012; Moreno-Mateos et al. 2012).

A small number of urban municipalities intentionally discharge secondarily treated wastewater into designated natural "assimilation" wetlands as an alternative to implementing advanced treatment technologies or constructed wetlands at WWTPs. These natural assimilation wetlands have been observed to facilitate nitrogen retention through a variety of biogeochemical processes, but the efficacy of such an approach is dependent on the relative Nr loading rate to area of high-functioning wetlands downstream (Day et al. 2004). Since the development of many coastal cities has been associated with extensive landfilling of natural wetlands and degradation of remaining coastal habitat (Lee et al. 2006; O'Meara, Thompson, and Piehler 2015), this type of complete replacement of WWTPs by natural ecosystems to facilitate N_r regulation would not be feasible in most large or densely populated coastal cities. However, the remaining natural ecosystems in highly urbanized coastal environstill be providing significant but ments may

unrecognized N_r regulation services, with implications for water quality and global biogeochemical cycling.

Denitrification and anammox in urban coastal ecosystems

Within coastal ecosystems, Nr can be sequestered through assimilation into biomass or burial in sediments, resulting in temporary regulation that can provide benefits for local ecological function (Herbert 1999; McGlathery, Sundbäck, and Anderson 2007). For this review, we will focus on heterotrophic denitrification and anammox (Figure 3), given their importance for long-term, multi-season regulation of nitrogen (Bonaglia et al. 2014). Through both of these processes, microbes respire using oxidized forms of Nr $(NO_3^-, NO_2^- \text{ or } N_2O)$ as terminal electron acceptors in the absence of oxygen, converting these reactive forms into N₂. With heterotrophic denitrification (commonly referred to simply as "denitrification"), organic carbon is utilized as the electron donor. Anaerobic ammonia oxidation (commonly known as



Figure 2. Natural (dendritic) tidal creeks and ditched (perpendicular) channels shown in a digital elevation model of two salt marsh islands of Jamaica Bay. Ditching was commonly used for mosquito control in urban wetlands during the twentieth century, but may unintentionally impact nitrogen regulation by enhancing tidal flushing and/or modifying macroinvertebrate community structure. Land elevation data are from the USA Geological Survey (USGS) 1m National Elevation Dataset https://lta. cr.usgs.gov/NED.

"anammox") is an autotrophic process, where NH_4^+ is used to reduce NO_2^- to N_2 and is itself oxidized to N_2 in the process (Engström et al. 2005). Along with anammox, the use of reduced inorganic sulfur, iron, or hydrogen as electron donors for autotrophic denitrification has been observed in natural systems (Straub et al. 1996; Shao, Zhang, and Han-Ping Fang 2010; Robertson and Gijs Kuenen 1983; Li et al. 2015), but have been poorly studied in coastal ecosystems (Damashek and Francis 2018).

Denitrification occurs as a multi-step process through which NO3⁻ is sequentially reduced to NO2⁻, N2O, and finally N2. Production of the different enzymes necessary to conduct each step of this process is encoded in genes that are widespread among the diverse bacteria of coastal ecosystems, although some are only able to complete part of the denitrification pathway (Zumft 1997). Under some environmental conditions, the full sequence of denitrification may not be completed, resulting in the emission of N2O, a potent greenhouse gas, rather than N₂. When anthropogenic N_r is available in more reduced forms (NH4+ or organic N), it must first be nitrified (and in the case of organic-N, also mineralized) before denitrification can take place. Coupled nitrification-denitrification often plays a substantial role in the regulation of N_r in coastal systems (Seitzinger 1988) and may be particularly important in systems that receive NH_4^+ -rich WWTP effluent, but its occurrence is dependent on patterns of redox zonation that allow these reactions to take place in close proximity.

While denitrification has been studied for nearly half a century, observations of anammox were first published in 1995 (Mulder et al. 1995). Since then, there has been great interest in its occurrence in natural systems and potential role in Nr regulation. Although anammox bacteria have been frequently observed in coastal sediments, its generally thought that in systems where labile organic carbon is abundant, such as eutrophic coastal sediments, denitrifying bacteria will outcompete anammox bacteria for NO₂⁻ (Table 1). However, under some physicochemical conditions, denitrification and anammox can actually be complementary, rather than competitive, with denitrification of NO3⁻ providing sufficient NO2⁻ to support further reduction through both denitrification and anammox (Hietanen and Kuparinen 2008; Nicholls and Trimmer 2009). Although our understanding of the environmental controls on the relative importance of these pathways is still an active research area (Table 1), recent studies



Figure 3. Simplified representation of nitrogen cycling processes in coastal ecosystems.

suggest that anammox should not be neglected as an N regulation pathway in urban coastal ecosystems (Hou et al. 2015b; Crowe et al. 2012).

Fate and transport of N_r across urban coastal habitats

The total amount of anthropogenic N_r that can be converted to N₂ is not only dependent on rates of denitrification and anammox at any given point in space, but also on the mass flux of N_r through zones where these reactions are favorable. For example, a saline tidal creek may be underlain by anoxic, organic-rich sediments with high potential rates of denitrification and anammox when Nr is available, but NO₃⁻ and NH₄⁺-rich effluent delivered from a sewer outfall may be transported as a lower density freshwater plume at the surface, never making contact with the sediments in which denitrification can occur. Across any given coastal landscape, Nr regulation will be dependent on the types of habitat present, their function, and areal extent (Smyth et al. 2013; Eyre et al. 2011), and it is important to understand the complex patterns of circulation and transport of Nr through the ecosystem and its subsurface. In temperate coastal waterways, salt marsh wetlands and benthic sediments can be important habitat to facilitate N regulation.

Coastal salt marsh

In fringe wetlands, subterranean groundwater may pass through or immediately below the salt marsh rhizosphere as it flows toward the coast, which can facilitate substantial N_r removal through denitrification (Santoro 2010). In coastal zones where the direct discharge of groundwater N_r is a significant contributor to the total anthropogenic load, the rhizosphere of perimeter salt marsh may serve as an important sink for upland-derived N_r , preventing it from being transported to N_r -sensitive receiving waters (Addy et al. 2005). In densely populated coastal zones, this reactive zone may be completely bypassed when N_r is primarily discharged directly into the water column through engineered outfalls. In these systems, the N_r regulation potential of salt marsh – including both fringe and island wetlands – will instead be largely determined by the mass flux of coastal water column N_r back into the bioactive zones within the salt marsh through tidal inundation and flushing.

To understand the potential for salt marsh to treat water column Nr, 3 primary "zones" of Nr removal within these wetlands (Figure 4) must be considered: the ponded water and shallow sediments at the surface of the vegetated platform, the rhizosphere, and the unvegetated sediments of tidal channels that interweave the marsh system (Koop-Jakobsen and Giblin 2010). Nr removal within a given salt marsh ecosystem will vary with fluxes of water into and between these zones, driven by tidal pumping, bioirrigation, and transpiration-driven advection (Bachand et al. 2014; Xin et al. 2009, 2012). The shallow sediments of the vegetated marsh platform are periodically inundated by tidal waters, which can support development of the anoxic conditions needed for denitrification to occur in the surficial sediments. Across any given marsh platform, the frequency of inundation will vary with elevation. Low marsh on



Figure 4. Hypothetical cross-section of a coastal salt marsh showing potential transport pathways of water column N and sites where denitrification may occur.

the coast or adjacent to tidal channels will be inundated daily with the high tide, while high marsh further inland may only be inundated during storm events or the highest tides of the metonic cycle. At low tide when marsh surficial sediments are reaerated, conditions can become favorable for NH_4^+ , to be converted to NO_3^- through nitrification, and subsequently removed through denitrification (Eriksson et al. 2003). In systems where NH_4^+ makes up a large fraction of the N_r load, such as those that receive WWTP effluent, the coupling of nitrification with denitrification over tidal cycles may result in greatly increased total rates of transformation of N_r to nonreactive N_2 .

When the marsh platform is inundated, ponded water can percolate vertically into the rhizosphere, facilitated by bioturbation, transpiration-induced advection, and tidal flushing (Aller 2001; Xin et al. 2012; Bachand et al. 2014). However, the actual mass flux of Nr into the salt marsh rhizosphere will be highly dependent on the geomorphology and stratigraphy of a given salt marsh, which often varies considerably from site-to-site (Wilson and Gardner 2006). The highly organic sediments at the surface of salt marsh may have very limited vertical permeability, which may serve as a constraint on the mass flux of ponded water and N_r that can penetrate deeply (Koop-Jakobsen and Giblin 2010). Thus, although denitrification rates in marsh surficial sediments may be high, the landscape-scale role of this zone in the removal of water column N_r can be limited by its relatively small volumetric extent in the absence of strong tidal flushing or extensive bioirrigation (Hughes, Binning, and Willgoose 1998).

Below the surface of salt marshes, the roots of wetland plants transport oxygen and exude organic

carbon, both of which facilitate high rates of coupled nitrification–denitrification (Sousa et al. 2012; Dollhopf et al. 2005; Sherr and Payne 1978). The depth of the rhizosphere of many temperate wetland plants may provide an extensive volume throughout which these high rates of N_r may occur. The rhizosphere of the common cordgrass *Spartina alterniflora* frequently extends down to at a depth of 20cm or more (Mozdzer et al. 2016). For common reed *Phragmites australis*, roots can extend to depths of 85cm, with significant biomass of the rhizosphere found more than 40cm deep in more saline systems (Moore et al. 2012).

Within the marsh platform, the relationship between sediment texture and the facilitation of denitrification in the rhizosphere is complex. Sandy soils are more permeable and can support the advective transport of tidal water deep into the salt marsh rhizosphere (Xin et al. 2012) but the rapid transport of porewater through the rhizosphere may limit nitrogen removal (Sparks, Cebrian, and Smith 2014). Mud or clay soils often contain more organic matter that can support enhanced rates of denitrification, but are generally less permeable, particularly in the vertical direction, resulting in reduced percolation of ponded water relative to coarse grained soils (Freeze and Cherry 1979).

The sediments of salt marsh tidal creeks and ditches may also provide important sites for N_r removal through denitrification (Vieillard et al. 2012, Eriksson et al. 2003). Although denitrification rates in unvegetated sediments will generally be lower than those with emergent vegetation (Alldred and Baines 2016), the sediments of subtidal creeks remain in constant contact with N_r in the water column (Koop-Jakobsen and Giblin 2009b), which may

provide the contact time necessary to facilitate denitrification. For intertidal creek sediments and mudflats, periodic inundation of these sediments can facilitate nitrification during low tide and denitrification at high tide (Smyth et al. 2013).

Relatively few studies published to date have investigated rates of anammox in coastal salt marsh. Koop-Jakobsen and Giblin (2009a) found that anammox was an insignificant (< 3%) contributor to N_r conversion to N₂ in marshes of Plum Island Sound, USA, and that modest fertilization with NO3⁻ did not increase the rate or relative importance of anammox in their study sites. In studies of salt marsh sediments from the highly urbanized and eutrophic Yangtze Estuary, Hou et al. (2013) and Zheng et al. (2016) observed a slightly higher relative contribution by anammox (4-14% of N₂ generated). In both of these studies, rates of anammox may have been underestimated due to the co-occurrence of dissimilatory nitrate reduction to ammonia (DNRA; Koop-Jakobsen and Giblin 2010), which can mask the occurrence of anammox measured using the isotope pairing technique (Song et al. 2016).

Eutrophication and human management activities can both significantly impact Nr regulation through denitrification and anammox in urban salt marshes. For example, extensive ditching or runnelling of salt marsh for mosquito control can significantly augment tidal flushing and the penetration of tidal water into the bioactive salt marsh rhizosphere (Lee et al. 2006), which could enhance areal denitrification rates. At the same time, these practices can have complex effects on the communities of emergent vegetation and burrowing invertebrates, with poorly understood implications for the hydrology and nutrient cycling of salt marsh ecosystems (Gedan, Silliman, and Bertness 2009). The impacts of open marsh water management on nutrient cycling has not been widely studied, but in observations of salt marsh in Barnegat Bay in the USA, denitrification rates in the vegetated sediments where dredged sediment had been sprayed were observed to be twice as high as those of adjacent vegetated marsh sediments (Velinsky et al. 2017).

In urban areas where marshland is being restored, the impacts of marsh restoration practices on the ability of these habitats to provide N_r regulation services also remain poorly understood. Sparks et al. (2015) observed that while the extent of vegetation coverage in restored sites did not significantly affect denitrification, marsh restoration on sandy sediments was not able to support significant denitrification, which they attributed to the short residence times and low organic matter content characteristic of sandy sediments (Sparks, Cebrian, and Smith 2014). Etheridge, Burchell, and Birgand (2017) observed significant N_r retention in field studies of restored coastal marshes but did not make the distinction between removal through denitrification or anammox and retention through processes such as plant uptake.

While salt marshes can provide significant N_r regulation services in coastal ecosystems, exposure to high N_r loading rates can result in the destabilization and, in some cases, areal loss of these habitats. Under high Nr loading conditions, common salt marsh plants often reapportion their growth from their roots and rhizosphere to their aboveground shoots, which is generally attributed to the reduced need for these plants to forage for this nutrient belowground when it is abundant in the water column (Turner et al. 2009; Levin, Mooney, and Field 1989). Since the shear strength of marsh soils is directly related to live belowground biomass (Sasser et al. 2017), salt marshes with reduced root biomass in eutrophic waterways are more susceptible to the erosive forces of waves and tides. This, in turn, can lead to marsh collapse and die-back resulting in both the permanent loss of ecosystem services provided by the marsh and the release of N_r that had been stored as peat within the salt marsh (Turner 2011).

The reduction in root biomass in response to high Nr loading has been observed in multiple studies of human-impacted coastal systems (Darby and Eugene Turner 2008; Watson et al. 2014; Graham and Mendelssohn 2014; Deegan et al. 2012; Alldred, Liberti, and Baines 2017; Valiela 2015). In two longterm ecosystem fertilization studies, the reduced belowground biomass in wetlands dominated by Spartina alterniflora was also observed to be accompanied by marsh collapse and areal loss (Valiela and Cole 2002; Deegan et al. 2012). The ability for an urban salt marsh to remain stable and continue to provide ecosystem services through high Nr loading is likely to be dependent on a variety of site-specific factors, including the initial elevation of the marsh, the magnitude of erosive forces through tide and wave action, vegetation species composition, and the character of Nr loading, although the relative importance of these factors remains uncertain.

Benthic sediments

Although salt marsh habitat can support particularly high denitrification rates, the extensive surface area of benthic sediments within coastal ecosystems allows for it to play an important role in N regulation at the landscape-scale (Jickells et al. 2014). To understand the ecosystem services provided by benthic sediments, their areal extent within a system must be considered along with the rates of denitrification or anammox that they facilitate. For example, although denitrification rates were higher in the muddy, fine-textured sediments of the Elbe Estuary and German Bight, the more extensive area of coarse-grained permeable sediments contributed to a greater percentage of systemwide N_r removal (Neumann et al. 2017).

It was historically assumed that NO_3^- supply would be limited at depth and benthic denitrification occurred only in shallow sediments. Recent research, however, has revealed that there can be substantial cycling of water between the deep sediments of submarine aquifers and the water column (Huettel, Berg, and Kostka 2014; Beebe and Lowery 2018). The impact of submarine groundwater mixing on system-scale benthic denitrification has been poorly quantified (Liefer et al. 2014), but may play an important role in understanding the N_r regulation services of benthic habitats.

Along with denitrification, many recent studies have investigated the role of anammox in benthic N-cycling and observed wide variation in its average rate and relative importance in urban and eutrophic benthic sediments. While all studies published to date have found that benthic anammox was relatively less important than benthic denitrification in N_r-removal; (0-33% of total N₂ production; Rich, Dale, Bongkeun Song, and Ward 2008; Crowe et al. 2012; Teixeira et al. 2014, 2012, 2016; Yin et al. 2015; Deng et al. 2015; Trimmer, Nicholls, and Deflandre 2003; Nicholls and Trimmer 2009; Song et al. 2016; Brin, Giblin, and Rich 2014), it was still a significant contributor to system-wide benthic N_r-regulation at several of the sites investigated. Anammox was first observed in a WWTP (Mulder et al. 1995), and it has been hypothesized that WWTP effluent can serve as a source of anammox bacteria in the natural environment (Dale, Tobias, and Song 2009). The benthic sediments immediately downstream of WWTP or CSO outfalls may be hot spots for the occurrence of anammox, with "hot moments" occurring during overflow or similar events that may provide a niche for which anammox bacteria are well-adapted (Babbin, Jayakumar, and Ward 2016; Babbin and Ward 2013).

Case study: Jamaica Bay, New York, USA

Jamaica Bay, a coastal lagoon located in New York City (Figure 5), provides an example of the relevance of the issues discussed here to the sustainable management of ultra-urban coastal systems. Over 2.2 million people reside in the bay's highly impervious, 310km² watershed, and its morphometry has been radically altered to support urban development and navigation over the past two centuries. Physiographic alterations to the Bay during the early twentieth century included filling of the numerous streams and wetlands that originally fringed its perimeter, dredging of deep channels for navigation and landfill supply, shoreline hardening, and the extension of the enclosing Rockaway Peninsula. These geomorphic changes have resulted in an increased baywide mean tidal range compared wide pre-development (Swanson et al. 2008).

Jamaica Bay is brackish and its freshwater supply is dominated (~ 90%) by point-source discharges from four WWTPs along its perimeter, with episodic discharge through CSOs during heavy rain events (Benotti, Abbene, and Terracciano 2007). Jamaica Bay receives continuous loading of N_r, primarily as NH4⁺, through WWTP effluent (Benotti, Abbene, and Terracciano 2007; Figure 6). Atmospheric deposition of Nr in Jamaica Bay and its watershed has not been directly measured. Using the highest areal Nr deposition rate estimated by Du et al. (2014) for the Northeast USA (26kg N ha^{-1} yr⁻¹), atmospheric Nr deposition would account for, at most, ~ 17% of Jamaica Bay's total Nr inputs (Table 2). This estimate includes the deposition of NH₃ generated by vehicular traffic along with NO_x (Bettez and Groffman 2013). In response to concerns about water quality and the stability of remaining salt marsh habitat, Nr management has become a high priority issue for local environmental managers. New York City has committed \$187 million to WWTP infrastructure upgrades since 201X to halve annual Nr loads, and while work completed so far has resulted in substantial N_r-load reductions, the N_r loading to the Bay remains high - in 2014, it was estimated at 4.5x10⁶ kg yr⁻¹ (NYC DEP, Unpublished, December 2016; Table 2).

As a result of Jamaica Bay's very high wastewater Nr loading, water column Nr concentrations in the Bay can exceed 100 μ mol L⁻¹, with the highest concentrations found in the tributary tidal creeks that receive wastewater treatment plant effluent (Figure 7). Jamaica Bay is eutrophic and, prior to the WWTP upgrades, phytoplankton blooms could reach very high densities (> $100\mu gL^{-1}$ chlorophyll *a*; Wallace and Gobler 2015). Northeast sections of the bay have historically experienced hypoxia during the summer, and the water column has been observed to be relatively acidic in many parts of the bay during the warm season due to enhanced decomposition (Wallace et al. 2014). In shallow areas of the bay where light is not limiting > 60% of the benthic surface is covered with Ulva sp., opportunistic macroalgae that are commonly found in eutrophic temperate estuaries and known to impact redox conditions and benthic nitrogen cycling (Wallace and Gobler 2015). Beneath Jamaica Bay, there is substantial circulation of baywater through the permeable sediments of the submarine aquifer, and porewater concentrations are enriched with dissolved inorganic nitrogen compared with the water column, suggesting that buried organic matter is remineralized (Beck et al. 2007). Like many urbanized areas, levels of dissolved trace metals in the water



Figure 5. Map of the Jamaica Bay Watershed, which includes locations of Waste Water Treatment Plant (WWTP) Facilities and CSOs. Vegetation coverage is modified from the Ecological Covertype Map, Version 2, developed by the Natural Areas Conservancy (O'Neill-Dunne et al. 2014). The vegetation layer is only available for New York City. Impervious cover data is from the 2011 National Land Cover Database (Homer et al. 2012).



Figure 6. N loading from the 4 Waste Water Treatment Plants (WWTPs) in the Jamaica Bay Watershed. Data from the EPA ECHO Monthly Discharge Monitoring Report (https://cfpub.epa.gov/dmr/index.cfm).

column of Jamaica Bay are highly increased relative to offshore water, which has been attributed to its industrial history along with continued inputs through sewer discharges (Beck, Kirk Cochran, and Sañudo-Wilhelmy 2009). In addition, a variety of pharmaceuticals and their human metabolites are ubiquitous throughout the sediments and water column of Jamaica Bay, but their influence on biogeochemical cycling has not yet been studied (Benotti and Brownawell 2007; Lara-Martín et al. 2015).

While over 90% of Jamaica Bay's historic wetlands have been lost to urban development, the remaining 22km² of island and perimeter marshes serve as an important ecological resource to local residents and a critical stopover for migratory birds on the Atlantic

Table 2. Jamaica Bay sources of Nr

| | | · 1. | |
|---|--|---------------------------------|---|
| Jamaica Bay N _r Source | Estimated Annual Load (kg N yr ⁻¹) | % of Total Annual Load | Estimation Source/ Approach |
| Wastewater Treatment Plants (WWTPs) | 4.5x10 ⁶ | 76.3 | NYC DEP, Unpublished, December 2016 |
| Atmospheric Deposition | 9.8 x10⁵ | 16.5 | Du et al. 2014 (Using highest value observed for Northeast United States) |
| Groundwater Discharge | 2.5 x10 ⁵ | 4.3 | Benotti, Abbene, and Terracciano 2007 |
| Combined Sewer Overflows (CSOs) | 8.9 x10 ⁴ | 1.5 | Benotti, Abbene, and Terracciano 2007 |
| Subway Dewatering (pumped water bypasses WWTPs) | 8.4 x10 ⁴ | 1.4 | Benotti, Abbene, and Terracciano 2007 |
| Landfill Leaching | ~ 0 | ~ 0 | Assumed to be negligible following landfill capping and remediation over the past decade. |
| Total Nr input to Jamaica Bay: | 5.9x10 ⁶ | | • |

Flyway (NYCDEP 2007). The islands and low marsh are dominated by Spartina alterniflora, while Spartina patens and Distichlis spicata are dominant in the high marsh. The invasive Phragmites australis is also common in many of the perimeter marshes (Figure 5). While the loss of Jamaica Bay's perimeter wetlands was largely the result of filling and urban land use conversion in the early twentieth century, the area of island salt marsh has been decreasing at an accelerated rate since the second half of the twentieth century, with over 60% of the 1951 island marsh area lost by 2003 (Robert 2001). The cause of this extensive marsh loss remains poorly understood, but likely includes the synergistic impacts of marsh destabilization under high nitrogen loading and the amplified tidal range (Wigand et al. 2014). To restore this lost habitat, environmental managers have piloted the direct replenishment of degraded marshes at five island sites. Marsh restoration involves the use of slurried sand from nearby dredging activities to raise the elevation of the marsh, followed by planting with native vegetation (Kress et al.).

Few field studies of ecological Nr regulation in Jamaica Bay have been published to date. Cornwell et al. (1999) reported net benthic N_2 flux rates of 122 μ mol N m⁻² hr⁻¹ in Jamaica Bay. Assuming similar rates for the 67 km² of Jamaica Bay bottom sediments, this would result in an annual Nr removal rate of 9.8×10^5 kg yr⁻¹ or ~ 22% of the total WWTP N_r load in 2012, following the first stage of implementation of WWTP upgrades. This N_r removal efficiency is very similar to results obtained for natural habitats of the Colne Estuary and Wadden Sea, which also receive comparable areal loads of anthropogenic nitrogen (Table 3). However, as discussed throughout this review, actual nitrogen removal rates in natural systems are highly variable in both space and time and may be misrepresented through the simple areal extrapolation approach, even when sediment textures and hydrodynamic forcing of sediment porewater



Figure 7. Annual median (a) NO_3^- and (b) NH_4^+ measured in Jamaica Bay surface waters in 2013. Data from the Jamaica Bay Water Quality Database (City University of New York (CUNY) Brooklyn College, Center for International Earth Science Information Network (CIESIN) Columbia University, New York City Department of Environmental Protection (NYCDEP), and National Park Service (NPS) 2017), see http://www.ciesin.columbia.edu/jbwq/parameters.html for detailed sampling methods.

exchange are considered (as in Gao et al. 2012). These can include "hot moments" with variation in temperature and N_r loading, the effects of urban pollutants on denitrification and anammox and feedbacks between hypoxia and nitrogen removal.

While several studies have addressed the impact of high N_r loads on the sustainability of Jamaica Bay's salt marsh (Wigand et al. 2014; Campbell et al. 2017), no published studies have investigated the N_r regulation services provided by these wetlands. There are currently no published field studies of denitrification in Jamaica Bay's salt marshes and a surface area-based assessment using rates available in the literature would suggest that they currently play a relatively limited role. The primary limitation on Nr removal in these systems is contact with tidal waters, which varies with elevation throughout the salt marsh systems of the Bay (Figure 6). Using the percentage of time that marshland area is inundated over the course of a year (see (Ensign, Piehler, and Doyle 2008) and denitrification rates measured in the near-surface sediments of New England Spartina alterniflora marsh by Koop-Jakobsen and Giblin (2010, 57.5 µmol N m⁻² hr¹), the annual Nr removed from inundating tidal water would be ~ 1.4×10^4 kg N yr⁻¹, or only ~ 1-2% of the annual Nr load from Jamaica Bay's WWTPs.

Based on the recent literature on environmental controls on salt marsh N_r regulation, this is likely to be an underestimate, and these wetlands may play a more significant landscape-scale role in N_r removal than indicated by area-based estimates alone, which is progressively lost each year as marsh area continues to decrease. There is currently insufficient information available on the marsh hydrogeology to inform the horizontal transport of water into the root zone or the effects of bioirrigation on advective transport. Some of the distinctly urban features of these marshes, such as

extensive ditching or amplified tidal flushing (Figure 8), may also actually enhance their ability to remove N_r at the same time as eutrophication and the high tidal range threaten their sustainability. As practitioners plan continued WWTP infrastructure upgrades, they do so without information on whether the upgrades will reduce N_r loads to levels that do not impact marsh stability, or to support the design of marsh restoration projects for enhanced denitrification and anammox.

Over the next few years, Jamaica Bay's environmental managers will be faced with many critical decisions, including the deployment of large-scale infrastructure or bathymetric re-contouring for flood resilience, investment in WWTP upgrades for further reductions in N_r loading and the restoration of lost or degraded wetland habitat. The recent advances in our understanding of N_r regulation mechanisms in coastal systems have the potential to inform this decision-making, but our understanding of key drivers and interactions in highly urbanized environments remains limited. However, the issues and challenges discussed here are not unique to Jamaica Bay, but are currently salient in many older coastal cities and can also provide important lessons for sustainable development of megacities.

Conclusions and research opportunities

The emergence of ecosystem services as an approach for valuation of natural processes has been one of the most exciting developments in ecology and environmental science over the past 20 years. Our review suggests that coastal ecosystems that receive high N_r loading through urban wastewater may be providing important N_r services. But, as demonstrated by the case study of Jamaica Bay, our understanding of how human activities affect these processes is limited and presents opportunities for cross-disciplinary

Table 3. Comparison of nitrogen removal efficiency in studies of urban coastal systems.

| | | · · · | | * | |
|--|---|---|--|---|--|
| Site | Area of Coastal Habit Considered (km ⁻²) | N load per unit area of coastal habitat (kg N km ⁻² yr ⁻¹) | % of N removed as N ₂ (through denitrification and anammox) | Approach | Study |
| Colne River Estuary, United Kingdom | 4.8 | 5.1x10 ⁴ (studies conducted from 1995 – 1998) | 18–27 (studies conducted from 1993–1995) | IPT | (N loads from (Dong, Nedwell, and Stott 2006)) |
| Wadden Sea, The (Gao et al. 2012) | Netherlands/ Germany | 14.7x10 ⁴ | 5.1 x10 ⁴ <i>to</i> 5.6 x10 ⁴ | ~ 30 | IPT |
| Elbe Estuary | Not provided | 4.7x10 ⁷ kg N yr ⁻¹ (areal rates not provided) | 11 (assuming the March- September average rate is also applicable from October-Februarv) | IPT | (Deek et al. 2013) |
| Jinpu Bay, China | 2,000 | 3.5 x10 ³ | ~ 20 | IPT | (Yin et al. 2015) |
| Barnegat Bay, NJ | 280 (including 110km ² of wetlands) | 2.4 x10 ³ | ~ 28 ± 7 | MIMS | (Velinsky et al. 2017) |
| Jamaica Bay, NY | 89 (including 22 km ² of wetlands) | 6.6 x10 ⁴ | ~ 17 | Rates obtained by Cornwell, Michael Kemp, and Kana 1999 (MIMS) and Koop-Jakobsen and Giblin 2010 (IPT) | This review |

IPT: Isotope Pairing Technique; MIMS: N2:Ar ratio approach using Membrane Inlet Mass Spectrometry



Figure 8. Tidal wetlands with % of example year inundated. Vegetation coverage is modified from the Ecological Covertype Map, Version 2, developed by the Natural Areas Conservancy (Forgione et al. 2015). The vegetation layer is only available for New York City and a small area of tidal wetlands outside the city's political boundary are excluded here. Water-level time series are from Year 2013 at USGS Tide Gage 01311850 (Jamaica Bay at Inwood). Vertical adjustments were made using vData version 3.3. Land elevation data is from the USGS 1m National Elevation Dataset.

environmental research. Particularly important topics for further study include:

- (1) Autotrophic denitrification in the urban coastal environment: Although most observational studies to date suggest that anammox plays a comparatively less important role than denitrification in coastal N cycling, recent studies suggest that there may be significant benefit in the continued investigation of autotrophic denitrification processes such as anammox in highly urban areas, particularly environments downstream of WWTP outfalls that are exposed to very high concentrations of water column NH4⁺. These locations may serve as autotrophic denitrification "hot-spots" for the removal of NH4⁺-N from the water column and may be an important complement to denitrification in regulating N_r systemwide.
- (2) Modeling nitrogen regulation in urban coastal systems: Recent advances in analytical and field methods now allow for improved quantification of denitrification and anammox rates both *in situ* (Koop-Jakobsen et al. 2009a) and through laboratory experiments (Song et al. 2016). However, they also present an opportunity to develop enhanced approaches for the upscaling of these

point measurements for long-term nitrogen budgets for coastal systems. As discussed throughout this review, rates of denitrification and anammox are highly variable between and within coastal landscapes, are dependent on complex and rapidly changing physical, chemical and ecological conditions, and are often dominated by hot spots and hot moments. The reliance on a single areal reaction rate for coastal habitats likely misrepresents their landscape-scale Nr regulation role and the incorporation of these phenomena into modeling has long been recognized as a challenge for the ecosystems research community (Groffman et al. 2009). Although increasingly advanced computational resources can play an important role in enhanced model development, there is also a need for the improved parameterization of ecosystem models, particularly to represent the unique water chemistry, hydrogeology, and human management activities associated with urban coastal systems.

(3) Identification of sustainable N_r loading thresholds: The very high N_r loading in many urban coastal systems often results in nitrogen "saturation syndrome," or reduced N_r regulation capacity (Drake et al. 2009; Eyre and Ferguson 2009). Enhanced modeling of coastal N_r budgets can support the identification of N_r loading thresholds that would facilitate sustained N_r regulation by natural systems. Using salt marshes as an example, below such a threshold, salt marsh ecosystems could be exposed to large fluxes of tidewater N_r and continue to support high rates of denitrification. Above this threshold, frequent exposure to high water column N_r would contribute to instability and collapse, with an unsustainable loss in salt marsh area.

While this review focused on N_r in temperate coastal systems, the implications can be extended to other urban coastal environments including subtropical and tropical ecosystems (Davis and Koop 2006; Rivera-Monroy et al. 2013) . They may also be particularly important for the many developing global cities that do not yet utilize WWTPs and are entirely reliant on the N_r regulation services provided by their natural systems. As urbanization continues to intensify along with increasing challenges from climate change, an enhanced understanding of the role of natural systems in the urban nitrogen cycle will be critical for both environmental management and global ecology research.

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