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REVIEW
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Processes and Microorganisms Involved in the Marine Nitrogen Cycle: Knowledge and Gaps

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Nitrogen (N) is a key element for life in the oceans. It controls primary productivity in many parts of the global ocean, consequently playing a crucial role in the uptake of atmospheric carbon dioxide. The marine N cycle is driven by multiple biogeochemical transformations mediated by microorganisms, including processes contributing to the marine fixed N pool (N_2 fixation) and retained N pool (nitrification, assimilation, and dissimilatory nitrate reduction to ammonia), as well as processes contributing to the fixed N loss (denitrification, anaerobic ammonium oxidation and nitrite-dependent anaerobic methane oxidation). The N cycle maintains the functioning of marine ecosystems and will be a crucial component in how the ocean responds to global environmental change. In this review, we summarize the current understanding of the marine microbial N cycle, the ecology and distribution of the main functional players involved, and the main impacts of anthropogenic activities on the marine N cycle.

Keywords: nitrogen processes, marine ecosystems, microbial community, functional nitrogen genes, anthropogenic activity, nitrous oxide

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INTRODUCTION

Nitrogen (N) is a key element for life and the functioning of marine ecosystems. It plays a crucial role in marine biogeochemistry, and because of its connections to the cycles of other elements such as carbon (C) it has a strong impact on Earth's climate (Gruber, 2008; Voss et al., 2013). Fixed N limits marine productivity in many parts of the global ocean. Its availability also regulates the strength of the biological pump, one of the mechanisms contributing to oceanic uptake of atmospheric C dioxide (CO_2) (Falkowski, 1997).

N is present in different oxidation states in the ocean, ranging from -III in reduced forms like ammonium (NH_4^+) and organic N to +V in fully oxidized nitrate (NO_3^-), which highlights its importance as both an electron acceptor and donor for energy metabolism in marine ecosystems (**Figure 1**). Microorganisms mainly mediate the redox transformations of N, changing the concentrations of N compounds in the environment. The major sources of fixed N for the ocean are biological N_2 fixation (BNF) and atmospheric deposition, while the major sinks are denitrification and anaerobic ammonium oxidation (anammox) (Gruber and Galloway, 2008). Because alterations of this balance caused by anthropogenic activity may pose significant impact on marine ecosystem health, biodiversity and climate change, the study of microbial communities involved in marine N cycling has gained great interest in recent years (Lam and Kuypers, 2011; Zehr and Kudela, 2011; Voss et al., 2013).

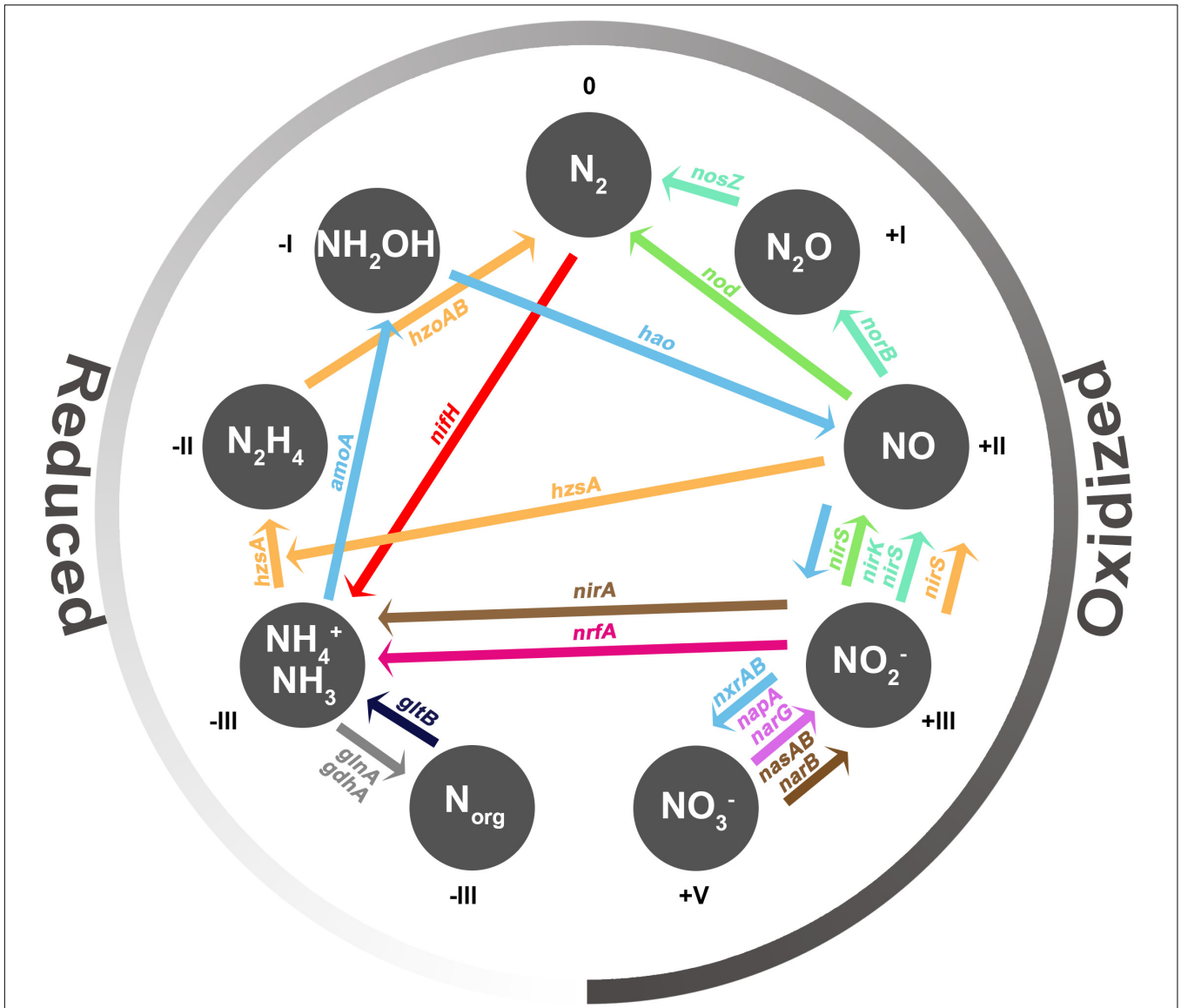

FIGURE 1 | Nitrogen species involved in N cycling and its transformations. Each gray circle represents a N species, and the number next to each N species indicates its oxidation state. Colored arrows represent each N transformation and the main marker genes involved: N_2 fixation (*nifH*) in red, nitrification (*amoA*, *hao*, *nxrA*, *nxrB*) in light blue, nitrate reduction (*narG*, *napA*) in violet, DNRA (*nrfA*) in magenta, assimilatory nitrate and nitrite reduction to ammonia (*nasA*, *nasB*, *narB, nirA*) in brown, ammonium assimilation (*glnA*, *gdhA*) in gray, remineralization (*gltB*) in dark blue, denitrification (*nirK, nirS, norB, nosZ*) in aquamarine, anammox (*nirS*, *hzsA*, *hzoA, hzoB*) in orange, and N-damo (*nirS, nod*) in green.

Microbial communities related to marine N cycling have been studied extensively using both culture-dependent and independent techniques. These technologies have allowed the attainment of a wealth of genomic data, revealing enormous metabolic versatility within N-transforming microorganisms. Furthermore, the study of genes encoding key metabolic proteins along with rate measurements of N processes has provided important discoveries about the genomic potential of microorganisms participating in N processes, as well as their biogeography and activity in marine systems (**Table 1**; Lam and Kuypers, 2011; Devol, 2015; Damashek and Francis, 2018). However, some discrepancies have been found between different studies, which may be due to the use of different methodologies (e.g., primer-based approaches versus untargeted approaches with meta-omic signatures or direct incubation experiments versus isotopic mass balance approach). As a contribution to this understanding, this review provides a general survey of the key microbial processes that comprise the marine N cycle and the N genes involved that are used as biomarkers, as well as the ecology and distribution of participating microorganisms in different marine ecosystems. We also identify several of the knowledge gaps that we still face in the study of microbial marine N processes. We end our review with a discussion

TABLE 1 | Representative studies using N cycling genes and rate measurements of N processes in marine ecosystems: ocean minimum zones, open ocean, deep-sea, and estuarine sediments.

Genes	Rates of N processes	Methods	Ecosystem	Condition tested	Major relationships	References
Key N genes	NH_3 and NO_2^- oxidation, denitrification, anammox	HC, ^{15}N-IPE, MG, qPCR, lipid profiles	ETNP OMZ	Relationship of N players between water column and particles at different depths	Niche partitioning of N players based on tolerance to O_2. Enrichment of denitrification genes associated with N_2O and N_2 production in particles	Fuchsman et al., 2017
AOA-*amoA*, *nxrB, nirS*, *Scalindua-nirS,* 16S rRNA	NO_2^- oxidation, NO_3^- and NO_2^- reduction, anammox	HC, qPCR, ^{15}N-IPE	Bay of Bengal OMZ	Evidence of N-loss processes	Denitrifier and anammox populations mediate low, but significant N loss. Low O_2 supports NO_2^- oxidation, restricting NO_2^- available for anammox or denitrification	Bristow et al., 2017
narG, 16S rRNA	NO_3^- and NO_2^- reduction	HC, SAG, qPCR, MG, MT	ETNP OMZ	Contribution of SAR11 to N cycling in OMZ	Great abundances of SAR11 lineages at anoxic depths, responsible of ∼40% of OMZ *nar* transcripts. SAR11 as important players of NO_2^- production in OMZs	Tsementzi et al., 2016
Key N genes	NH_3 and NO_2^- oxidation, NO_3^- reduction	HC, ^{15}N-IPE, MG, MT	Louisiana Shelf (Gulf of Mexico)	Links among NO_2^- accumulation, microbial taxa and metabolisms across O_2 gradients	NO_2^- accumulation in the hypoxic zone due to a decoupling of NH_3 oxidation and NO_2^- oxidation driven by temperature, O_2 and substrate availability	Bristow et al., 2015
Nitrospina 16S rRNA, *amoA*	NH_3 and NO_2^- oxidation, NO_3^- and NO_2^- reduction	HC, ^{15}N-IPE, IP, qPCR	ETNP OMZ	Cycling of NO_3^- and NO_2^- in the secondary NO_2^- maximum	50% of reduced NO_3^- to NO_2^- is re-oxidized back to NO_3^-. Anammox contributes to NO_2^- oxidation, but is not responsible for all of it	Buchwald et al., 2015
Key N genes, 16S rRNA	NH_3 and NO_2^- oxidation, denitrification, anammox	HC, ^{15}N-IPE, 16S Illumina, MG, MT	ETNP OMZ	Differences of N metabolic activities between particle-associated and free-living communities	N cycle activity, except denitrification, is confined to free-living communities that are dependent on particle access	Ganesh et al., 2015
nifH	BNF	HC, ^{15}N-incorporation, qPCR, RT-qPCR, pyrosequencing	Baltic Sea OMZ	Diversity and activity of heterotrophic diazotrophs	High diversity of active heterotrophic diazotrophs in anoxic NH_4^+-rich waters	Farnelid et al., 2013
Major N genes	NH_3 and NO_2^- oxidation, DNRA, denitrification, anammox	HC, ^{15}N-IPE, qPCR	ETSP OMZ	Role of organic matter export in N-loss	N cycling is linked to the export of organic matter. N-loss is most active over the shelf, fueled by sinking organic matter and benthic NH_4^+ release	Kalvelage et al., 2013

(Continued)

TABLE 1 | Continued

Genes	Rates of N processes	Methods	Ecosystem	Condition tested	Major relationships	References
nifH	BNF	HC, qPCR, clone libraries	ETSP OMZ	Occurrence of N_2 fixation in denitrified and oxygen-deficient waters	Diverse diazotrophs; high and temporal variable BNF in oxic and OMZ denitrified waters	Fernandez et al., 2011
nrfA, *nirS, Scalindua-nirS*	DNRA, anammox, denitrification,	HC, ^{15}N-IPE, RT-qPCR, CARD-FISH, clone libraries	Arabian OMZ	Mechanisms of biological N_2 production	Highly active anammox and hardly detectable denitrification. Anammox coupled to DNRA. N-loss rates linked to organic matter	Jensen et al., 2011
amoA, napA, narG, nirS, Scalindua-nirS, nrfA	NH_3 oxidation, DNRA, NO_3^- reduction, anammox	HC, ^{15}N-IPE, qPCR, RT-qPCR	ETSP OMZ	Microbial processes responsible for generation of NH_4^+ and NO_2^- for anammox	Anammox is the main N-loss pathway and obtains NO_2^- from NO_3^- reduction and aerobic NH_3 oxidation, and NH_4^+ from DNRA and remineralization *via* NO_3^- reduction. Deep-sea NO_3^- accounted for 50% of N loss	Lam et al., 2009
nirS, Planctomycetes 16S rRNA	Denitrification, anammox,	HC, ^{15}N-IPE, qPCR	ETSP, Arabian OMZ	Activity and abundance of denitrifiers and anammox bacteria	N_2 is mainly produced by denitrification in the Arabian OMZ and by anammox in the ESTP	Ward et al., 2009
amoA, Crenarchaeota 16S rRNA	NH_3 oxidation	HC, ^{15}N-IPE, qPCR, clone libraries	Gulf of California OMZ	Activity and abundance of NH_3 oxidizers	AOA are the most abundant within OMZ, where nitrification may be coupled to denitrification. AOB are low or undetectable. NH_3 oxidation correlated with AOA	Beman et al., 2008
Planctomycetes 16S rRNA	Anammox	HC, ^{15}N-IPE, FISH, clone libraries, lipid profiles	Namibian OMZ	Detection of anammox bacteria	Anammox is mainly responsible for N_2 loss	Kuypers et al., 2005
nifH	BNF	HC, ^{15}N-IPE, qPCR, Illumina	NPSG, CCS, ESP	Link between marine diazotrophic diversity and BNF rates	Distinct biogeographical patterns among the three regions. Diazotrophs are omnipresent in marine waters, but BNF is regionally restricted	Gradoville et al., 2017
nifH	BNF	HC, ^{15}N-IPE, MT, MT, qPCR	North Pacific	Diazotroph community structure and activity along a 7500 km south-north transect	Different diazotrophic composition between (sub)tropical gyre and cold northern regions, where BNF was also detected	Shiozaki et al., 2017
amoA	Nitrification	Light experiments, HC, ^{15}N-IPE, qPCR, RT-qPCR	Offshore Monterey Bay	Effect of light and phytoplankton growth on the activity of NH_3 oxidizers	Nitrification in the photic zone is more regulated by competition with phytoplankton for NH_4^+ than by light	Smith et al., 2014b

(Continued)

TABLE 1 | Continued

Genes	Rates of N processes	Methods	Ecosystem	Condition tested	Major relationships	References
amoA	NH_3 oxidation	HC, ^{15}N-IPE, qPCR, microarrays	Sargasso Sea	Depth distribution of NH_3 oxidation rates and NH_3 oxidizers	Maximum NH_3 oxidation rates at the PNM, where AOA outnumber AOB. Below the PNM AOB outnumber AOA. A diverse AOA community is linked to seasonal biogeochemical changes	Newell et al., 2013
amoA, 16S rRNA of MGI and *Nitrospina*	Nitrification	HC, IP, ^{15}N-IPE, RT-qPCR, clone libraries	CCS	Activity and distribution of nitrifiers and their contributions to N cycling	AOA outnumber AOB and are distributed in shallow/deep ecotypes. AOA and MGI abundances correlated with *Nitrospina* abundance. Nitrification is not correlated to *amoA* and produces 1.5–4 times the N_2O flux from deep water	Santoro et al., 2010
nifH	BNF, NH_4^+ assimilation	HC, ^{15}N-incorporation, ^{15}N-IPE, clone libraries	Deep-sea sediments	Activity and distribution of benthic diazotrophs	High and heterogeneous BNF that is inhibited by NH_4^+. Methane-coupled sulfate reduction dependency of BNF in seep sediments	Dekas et al., 2018
Planctomycetes 16S rRNA	Anammox	HC, ^{15}N-IPE, clone libraries, lipid profiles	Deep-sea hydrothermal vents	Role of anammox in hydrothermal vents	Active anammox bacteria in hydrothermal vents. Sequences suggest a new anammox clade	Byrne et al., 2009
amoA	Nitrification	Potential oxidation of NH_3, competitive PCR, clone libraries	Deep-sea cold seep sediments and water	Diversity and activity of NH_3 oxidizers	AOA outnumber AOB. Unique and psychrophilic AOA and AOB are responsible for nitrification in deep cold seep sediments	Nakagawa et al., 2007
Planctomycetes 16S rRNA	Anammox	HC, ^{15}N-IPE, FISH, clone libraries	Anoxic marine sediments and water	Diversity and activity of anammox bacteria in anoxic marine ecosystems	Ubiquitous presence of active anammox bacteria belonging to *Ca.* Scalindua in different anoxic environments	Schmid et al., 2007
NC10 16S rRNA, *pmoA*	N-damo	HC, IPE, clone libraries, qPCR	Zhangjiang estuarine sediments	Diversity and activity of n-damo bacteria in mangrove sediments	Widespread occurrence and high diversity of N-damo bacteria, which are more active and abundance in the upper layer	Zhang et al., 2018
nifH	BNF	HC, ^{15}N-incorporation, qPCR, RT-qPCR, illumina	Roskilde Fjord and the Great Belt strait	Diversity and activity of diazotrophs in two mesohaline temperate estuaries	Significant BNF mediated by heterotrophic, photoheterotrophic and photosynthetic diazotrophs that vary in space and time	Bentzon-Tilia et al., 2015

(Continued)

TABLE 1 | Continued

Genes	Rates of N processes	Methods	Ecosystem	Condition tested	Major relationships	References
napA, narG, nrfA, nirS, 16S rRNA	Denitrification, DNRA	HC, ^{15}N-IPE, 16S T-RFLP, qPCR, RT-qPCR,	Colne estuarine sediments	Spatial-temporal variation in the activity and abundance of denitrifying and DNRA community along a NO_3^- gradient	Denitrification, DNRA and corresponding gene abundances and transcripts decrease along the estuary without a temporal correlation	Smith C. J. et al., 2015
amoA, 16S rRNA	Nitrification	HC, nitrification potential, qPCR, DGGE, 16S pyrosequencing	Colne estuarine sediments	Spatial-temporal variation in the activity and diversity of AOA and AOB in surface sediments	Nitrification potential differs in space and time. AOB dominate over AOA, with AOB/AOA abundance increasing from the head to the mouth	Li et al., 2015
nrfA	DNRA	HC, ^{15}N-IPE, qPCR, pyrosequencing	New River estuarine sediments	Activity and diversity of DNRA community along a salinity gradient	Variation of DNRA community along the salinity gradient. DNRA bacterial abundance and organic carbon availability regulate DNRA activity	Song et al., 2014
Planctomycetes 16S rRNA	Anammox and denitrification	HC, ^{15}N-IPE, clone libraries, qPCR	Yangtze estuarine sediments	Anammox bacterial diversity and activity in marsh sediments	Salinity defines anammox bacterial distribution, whose activity is related to temperature, nitrite, and anammox bacterial abundance. Anammox is link to denitrification, which is the main N-loss pathway	Hou et al., 2013
nirK, nirS	Denitrification	HC, denitrification potential, qPCR, clone libraries	San Francisco estuarine sediments	Spatial-temporal variation in the activity and community structure of denitrifiers	*nirS* abundance correlated with denitrification and higher than *nirK* abundance at every site and time point. Salinity, organic carbon, N and several metals influence denitrification rates, *nir* abundance and community structure	Mosier and Francis, 2010
Planctomycetes 16S rRNA	Anammox and denitrification	HC, ^{15}N-IPE, clone libraries, T-RFLP, qPCR	Cape Fear River estuarine sediments	Spatial-temporal variation in the activity and diversity of anammox bacteria	Salinity influences diversity and abundance of anammox bacteria, which are linked to anammox rates	Dale et al., 2009
narG, napA, nirS, nrfA, Planctomycetes 16S rRNA	Denitrification, DNRA, anammox	^{15}N-IPE, NO_3^- reduction potential, qPCR, RT-qPCR, clone libraries	Colne estuarine sediments	Spatial variation and relationship between gene abundances and rates of denitrification, DNRA and anammox	Denitrification and DNRA rates decrease toward the mouth. DNRA potential and *nrfA* increase and denitrification potential and *nirS* decrease as NO_3^- declines. Anammox only detected at the head	Dong et al., 2009

(Continued)

TABLE 1 | Continued

Genes	Rates of N processes	Methods	Ecosystem	Condition tested	Major relationships	References
Planctomycetes 16S rRNA	Anammox and denitrification	HC, ^{15}N-IPE, clone libraries	Chesapeake Bay sediments	Relative activities of anammox and denitrification along salinity gradients	Anammox rate associated with *Ca.* Scalindua, contributes up to 22% of N loss in the freshwater portion and correlated with salinity and NO_3^-	Rich et al., 2008
amoA, 16S rRNA	NH_3 oxidation	HC, nitrification potential, qPCR	Sediments from six estuaries	Relationships between AOA and AOB abundances, potential nitrification and environmental variables	Potential nitrification correlated with AOA abundance, and its variability is predicted by salinity and pore water sulfide	Caffrey et al., 2007

BNF, biological N fixation; HC, hydrochemical data; IP, isotope profiles; IPE, isotope pairing experiments; MG, metagenomics; MT, metatranscriptomics; SAG, single amplified genomes; FISH, fluorescence in situ hybridization; ETNP, Eastern Tropical North Pacific; ETSP, Eastern Tropical South Pacific; OMZ, oxygen minimum zones; NPSG, North Pacific Subtropical Gyre; CCS, California Current system; ESP, Eastern South Pacific; AOA, ammonia-oxidizing archaea; AOB, ammonia-oxidizing bacteria; PNM, primary NO_2^- maximum.

of the impacts of anthropogenic activity on the microbially mediated marine N cycle.

MICROBIAL PROCESSES IN THE MARINE N CYCLE

The marine N cycle is driven by multiple microbial transformations, and N-converting enzymes are found in very diverse microorganisms globally distributed throughout marine systems (**Figure 2**). The microbial transformations of N compounds have important effects on the balance of marine and global N budgets. Thus, understanding how they occur, their distribution and the factors making them possible is essential to comprehend the fate of marine ecosystems and the future Earth. In this section, we give a general overview of the biochemistry and ecology of the main marine N processes and the microorganisms involved in them. In order

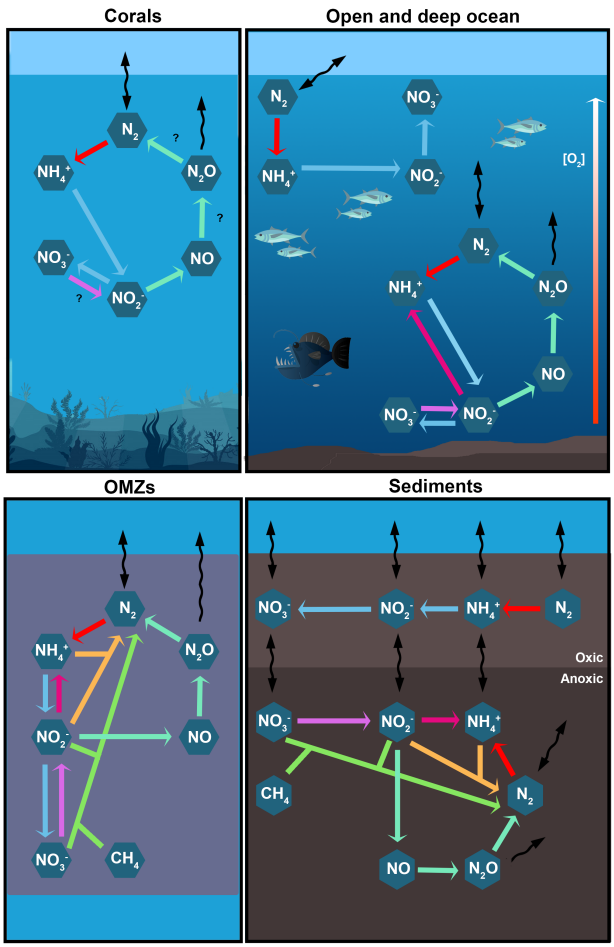

FIGURE 2 | The main studied processes of the N cycle in different marine environments. Every colored arrow represents a N transformation: N_2 fixation (red), nitrification (light blue), nitrate reduction (violet), DNRA (magenta), denitrification (aquamarine), N-damo (green), and anammox (orange). Black curved arrows represent physical processes such as advection and diffusion.

to emphasize the role of these processes in the marine and global budgets, we divide them into processes contributing to the marine fixed N (BNF) and retained N pool (derived from processes that transform one N species to another without causing its loss from the system) and processes contributing to the fixed N loss.

Bioavailable N-Gain and Retention Processes

BNF is the only biotic process adding N to marine systems and it has been estimated of ∼140 Tg N yr^{-1} (Eugster and Gruber, 2012; Luo et al., 2012). However, this estimate remains highly uncertain due to the incomplete knowledge of the organisms involved and their ecological controls (Gruber, 2016; Landolfi et al., 2018). Other microbial N processes such as nitrification, dissimilatory nitrate reduction to ammonia (DNRA) and N assimilation retain the fixed N. Most marine microorganisms can assimilate inorganic N forms, and also dissolved organic N compounds in estuaries and coastal waters (Damashek and Francis, 2018) and even in oligotrophic open ocean waters (Benavides et al., 2017b). Thus, addressing this process is beyond the scope of this review, but it is covered elsewhere (e.g., Allen et al., 2001; Zehr and Ward, 2002; Martiny et al., 2009; Zehr and Kudela, 2011; Damashek and Francis, 2018).

Biological N_2 Fixation (BNF)

Marine N_2 fixers (diazotrophs) convert dissolved N_2 gas into bioavailable ammonia (NH_3). This is an intensely energy-requiring process that only a small but diverse group of bacteria and archaea are able to carry out. Marine diazotrophs mainly include non-heterocystous filamentous cyanobacteria (e.g., *Trichodesmium, Oscillatoria*, *Lyngbya*), heterocystous filamentous cyanobacteria (e.g., *Aphanizomenon*, *Nodularia*), diatom symbiotic cyanobacteria (e.g., *Richelia, Calothrix*), and unicellular cyanobacteria (*Ca.* Atelocyanobacterium thalassa [UCYN-A], *Crocosphaera watsonii* [UCYN-B] and *Cyanothece* [UCYN-C]) (Villareal, 1991; Capone, 1997; Zehr et al., 2001; Thompson et al., 2012). UCYN-A is further divided into at least four sublineages; two of them (UCYN-A1 and UCYN-A2) live symbiotically with distinct prymnesiophyte microalgae (Zehr et al., 2016, and references therein). Other marine diazotrophs include heterotrophic bacteria (e.g., *Klebsiella*, *Vibrio*), phototrophic bacteria (e.g., *Chlorobium*, *Chromatium*, *Rhodospirillum*), strict anaerobes (e.g., *Clostridium*, *Desulfovibrio*), iron (Fe) oxidizers (e.g., *Thiobacillus*), methanogenic Euryarchaeota, and even members of Planctomycetes (Zehr and Paerl, 2008; Bombar et al., 2016; Delmont et al., 2018). These microorganisms share a common feature: the nitrogenase complex, which catalyzes N_2 fixation.

Nitrogenase is composed of two metalloproteins: the molybdenum (Mo)–Fe protein (dinitrogenase) encoded in the *nifDK* genes; and the Fe protein (dinitrogenase reductase) encoded in the *nifH* gene. Alternative nitrogenases replace Mo with vanadium or solely contain Fe, and are encoded in the *vnf* and *anf* genes, respectively (Zehr et al., 2003). The *nifH* gene is the preferred biomarker in the study of diazotroph diversity because it remains highly conserved (Zehr et al., 2003; Turk et al., 2011; Jayakumar et al., 2012).

Factors affecting BNF in marine systems

Oxygen (O_2), light, temperature, inorganic N forms, phosphorus (P), Fe, and organic matter are the main factors that affect marine diazotroph distribution. Nitrogenase is sensitive to O_2, and diazotrophs have developed numerous protective strategies against this. For example, several cyanobacteria generate specialized N_2-fixing cells called heterocysts that provide an almost anoxic environment. Temporal separation is another protection mechanism; most photosynthetic diazotrophs and certain proteobacterial diazotrophs fix N_2 at night (Moisander et al., 2014), whereas *Trichodesmium* and heterocyst-forming cyanobacteria fix N_2 during the day (Staal et al., 2007). The ability of *Trichodesmium* to fix N_2 during daytime remains enigmatic. Several mechanisms have been considered, such as its nitrogenase is confined to specialized cells called diazocytes (Bergman and Carpenter, 1991), the photoreduction of O_2 to H_2O in the photosystem I (the Mehler reaction) (Milligan et al., 2007), the uncoupling of CO_2 and N_2 fixation in cyanophycin granules (Finzi-Hart et al., 2009), or the down-regulation of photosynthesis during the period of maximum nitrogenase activity at midday (Berman-Frank et al., 2001b), which suggests that light may also be a determinant factor for BNF. Interestingly, the symbiosis between UCYN-A (which lacks genes for oxygenic photosynthesis and C fixation, Zehr et al., 2008) and its algal host has led to enable daytime BNF (Muñoz-Marín et al., 2018), although *nifH* expression of UCYN-A has also been observed at night (Moisander et al., 2014).

Temperature is an important factor determining the distribution of different diazotrophs in the ocean. *Trichodesmium* appears to be distributed mainly in (sub)tropical surface waters (Capone, 1997); while small diazotrophs have been found in a wider latitudinal span (Moisander et al., 2010; Luo et al., 2012), from colder surface waters (e.g., Holl et al., 2007; Fernández-Méndez et al., 2016; Harding et al., 2018) to (sub)tropical marine waters (e.g., Bonnet et al., 2009; Messer et al., 2016; Berthelot et al., 2017; Stenegren et al., 2018). It is important to note that temperature may be correlated with other factors that control the distribution patterns of marine diazotrophs such as light, NO_3^- or O_2 (Stal, 2009; Sohm et al., 2011b).

There is increasing evidence that BNF may not be as sensitive to inorganic N as previously thought (Dekaezemacker and Bonnet, 2011; Turk-Kubo et al., 2018), especially when P is not limited (Knapp, 2012). P availability influences BNF (e.g., Riemann et al., 2010; Gradoville et al., 2017) and the distribution of diazotrophs (Sohm et al., 2011b). For instance, cyanobacterial diazotrophs have been associated with high P concentration in the Arctic Ocean (Fernández-Méndez et al., 2016) and the Baltic Sea (Moisander et al., 2007b). High BNF might be also associated with denitrified waters in oxygen minimum zones (OMZs), which are limited in N relative to P (Deutsch et al., 2007; Fernandez et al., 2011; Loescher et al., 2014). Thus, N:P ratio may play a critical role, as BNF rates at high inorganic N concentrations can be offset when P is available (Knapp et al., 2012).

Diazotrophs require much more Fe for growth than other microbes, and its bioavailability directly affects BNF in many areas of the ocean (Berman-Frank et al., 2001a; Kustka et al., 2002; Knapp et al., 2016). Fe is generally depleted in surface waters of the open ocean, and Fe additions can stimulate diazotrophic activity (Turk-Kubo et al., 2012); thus the delivery of dust rich in Fe to the ocean may ultimately control the rate and distribution of marine BNF (Monteiro et al., 2011; Sohm et al., 2011b). For instance, diazotrophs, especially *Trichodesmium*, are abundant in the North Atlantic Ocean, in which dissolved Fe concentrations are relatively high because dust inputs are greater than in the South Atlantic Ocean, where dissolved Fe concentrations are extremely low (Langlois et al., 2008; Moore et al., 2009). Furthermore, direct experimental measurements have demonstrated that marine BNF can be co-limited by both Fe and P availability (Mills et al., 2004).

Finally, dissolved organic matter seems to stimulate heterotrophic diazotrophs in aphotic environments (Bonnet et al., 2013; Rahav et al., 2013; Benavides et al., 2015, 2016a) and coastal waters (Bentzon-Tilia et al., 2015; Severin et al., 2015) due to the high-energy requirements of the reaction. Furthermore, the interior of C-rich particles may be suitable for heterotrophic BNF (Moisander et al., 2017; Farnelid et al., 2019; and references therein). Additionally, organic matter could promote the mixotrophic nutrition of *Trichodesmium* when inorganic nutrients are scarce (Benavides et al., 2017b).

Distribution of diazotrophs in marine environments

The global presence of diazotrophs has been documented in recent years (**Table 1**; Monteiro et al., 2010; Sohm et al., 2011b; Luo et al., 2012). BNF is not only present in tropical surface waters (Capone et al., 2005; Goebel et al., 2010), but also in hypoxic basins (Hamersley et al., 2011; Farnelid et al., 2013), OMZs (Fernandez et al., 2011; Jayakumar et al., 2012), deep sea (Dekas et al., 2009), hydrothermal vents (Mehta and Baross, 2006), the Arctic Ocean (Sipler et al., 2017; Harding et al., 2018) and coral reefs (Benavides et al., 2017a), as well as in estuaries and nutrient-rich coastal upwelling regions (Mulholland et al., 2012; Bentzon-Tilia et al., 2015). These discoveries have challenged the classical paradigm that diazotrophy is constrained to warm, oligotrophic, surface waters.

Open oceans. BNF is particularly important in extremely oligotrophic environments such as open-ocean gyres, in which bioavailable N is scarce (Karl et al., 2002; Halm et al., 2012). Much of the research on diazotroph distribution has focused on *Trichodesmium,* which is mainly found in the North and Tropical Atlantic Ocean and the Arabian Sea, where it often forms massive surface blooms (Capone et al., 1998, 2005). The dominance of *Trichodesmium* in warm oligotrophic waters of the Tropical Atlantic Ocean seems to be due to a reduction of the N:P ratio by an increased uptake of inorganic N forms by non-diazotrophic cyanobacteria (Goebel et al., 2010; Singh et al., 2017), while its dominance in the Northern Atlantic Ocean seems to be due to high dissolved Fe concentrations (Langlois et al., 2008; Moore et al., 2009).

Diatom symbiotic cyanobacteria have a much patchier distribution, probably because the diatom hosts require silicon to build their cell walls (Monteiro et al., 2010; Sohm et al., 2011b). They predominate in the warm ocean, with the largest densities in the plumes of Amazon (Foster et al., 2007), Congo (Foster et al., 2009), and Mekong rivers (Grosse et al., 2010).

UCYN groups display different distributions in the ocean. UCYN-A was originally described from partial *nifH* fragments recovered from the North Pacific (Zehr et al., 1998) and has been recently detected in all ocean basins (Cabello et al., 2016; Farnelid et al., 2016; Martínez-Pérez et al., 2016), where UCYN-A1 dominates and frequently co-occurs with UCYN-A3 in the (sub)tropical open ocean (Thompson et al., 2014; Turk-Kubo et al., 2017). UCYN-B has been also detected in the global ocean, but dominates in (sub)tropical surface waters (e.g., Zehr et al., 2007; Bonnet et al., 2015; Stenegren et al., 2018). UCYN-C seems to be constrained to (sub)tropical open regions (e.g., Goebel et al., 2010; Berthelot et al., 2017), where is adapted to low P and high salinity waters (Turk-Kubo et al., 2015; Cheung et al., 2017).

Heterotrophic diazotrophs are also important N_2 fixers in the global ocean (Bombar et al., 2016), where they are ubiquitous in the marine sunlit layer (Riemann et al., 2010; Farnelid et al., 2011; Langlois et al., 2015). Heterotrophic Proteobacteria are widespread in oceanic environments, but dominate in the Pacific coastal upwelling systems (Gradoville et al., 2017), the South Pacific Gyre (Halm et al., 2012), the Indian Ocean (Shiozaki et al., 2014), and the Arabian Sea (Kumar et al., 2017). Diverse and active heterotrophic diazotrophs are also found in sinking particles (Farnelid et al., 2019), aphotic waters (Hamersley et al., 2011; Bonnet et al., 2013; Rahav et al., 2013), OMZs (Jayakumar et al., 2012; Loescher et al., 2014; Fernandez et al., 2015), NH_4^+-rich sulfidic-anoxic waters of the Baltic Sea (Farnelid et al., 2013), and colder waters such as those in the Arctic Ocean (Blais et al., 2012; Fernández-Méndez et al., 2016), where *nifH* sequences related to anaerobic bacteria predominate (Farnelid et al., 2011; Shiozaki et al., 2018).

Estuaries and coastal zones. Little is known about the distribution and activity of diazotrophs in estuaries and coastal regions. BNF in these systems is affected by high nutrient inputs from land, so it is assumed to be unimportant (Howarth et al., 1988). However, recent studies suggest that BNF may be important in a number of estuaries and nutrient-repleted coastal upwelling regions (Fulweiler et al., 2007; Wen et al., 2017; Tang et al., 2019), where complicated relationships exist between environmental factors and distribution of different diazotrophs (Short et al., 2004; Moisander et al., 2007a; Severin et al., 2015). In the Baltic Sea, for instance, planktonic heterotrophic diazotrophs are common in a eutrophic estuary, while cyanobacterial diazotrophs are more abundant in a lower-nutrient estuary (Bentzon-Tilia et al., 2015). Furthermore, UCYN-A is the most abundant diazotroph in coastal upwelling ecosystems (Sohm et al., 2011a; Agawin et al., 2014; Moreira-Coello et al., 2019), and other nutrient-rich coastal waters (Mulholland et al., 2012, 2019; Shiozaki et al., 2015, 2017), where UCYN-A2 dominates and usually co-occurs with UCYN-A1 and sometimes with UCYN-A4 (Messer et al., 2015; Turk-Kubo et al., 2017; Henke et al., 2018). Additionally, diatom symbiotic cyanobacteria may be abundant in upwelling regions such as the Taiwan Strait (Wen et al., 2017).

BNF is also important in estuarine and coastal sediments, where heterotrophic bacteria are the dominant diazotrophs (e.g., Burns et al., 2002; Fan et al., 2015a). Finally, BNF is a key process in coastal microbial mats, whose diazotrophic community is composed mainly of filamentous cyanobacteria, anoxygenic phototrophic bacteria, and sulfate-reducing bacteria (Severin et al., 2010; Woebken et al., 2012, 2015).

Seeps and deep-sea vents. Mehta et al. (2003) provided the first evidence of *nifH* genes in deep-sea hydrothermal vents, where methanogenic archaea are the dominant diazotrophs (Mehta and Baross, 2006). Further, a consortium composed of an anaerobic methanotrophic archaeon (ANME) and a sulfate-reducing bacterium seems to mediate both sulfate-dependent anaerobic methane (CH_4) oxidation (S-damo) and BNF in CH_4 seep sediments (Dekas et al., 2009, 2014, 2018). Proteobacterial diazotrophs are also abundant in deep-sea hydrothermal vents (Wu et al., 2014; Cao et al., 2015) and CH_4 seep sediments (Dang et al., 2009b).

Coral reefs. Corals are found in N-depleted (sub)tropical coastal waters; thus, BNF should play an important role in these ecosystems, providing an additional source of N for symbiotic dinoflagellates and thus improving the productivity. Corals harbor diverse communities of diazotrophs consisting mostly of heterotrophic bacteria, which are host species-specific (Rädecker et al., 2015; Benavides et al., 2017a). Diazotrophs participate in coral nutrition by three main mechanisms: as endosymbionts fixing N_2 in several compartments of the holobiont (Olson et al., 2009; Lema et al., 2012; Grover et al., 2014), pelagic diazotroph ingestion (Benavides et al., 2016b) or N_2 fixation products assimilated by corals (Cardini et al., 2015). Additionally, the ecological importance of N_2-fixing symbionts may be determined by the trophic functional group of the host. For instance, Pogoreutz et al. (2017) found that autotrophic Pocilloporidae exhibited *nifH* copies and gene expression 100 times higher than those in heterotrophic Fungiidae, suggesting that BNF compensates for the low N uptake in autotrophic corals.

Nitrification

Nitrification is an aerobic process and involves three types of microorganisms: those who oxidize NH_3 to nitrite (NO_2^-), those who oxidize NO_2^- to NO_3^-, and those who completely oxide NH_3 to NO_3^- *via* NO_2^- (comammox, complete ammonia oxidation).

The oxidation of NH_3 is carried out by two groups of chemolithotrophic microorganisms: ammonia-oxidizing bacteria (AOB) belonging to a few genera within the Betaproteobacteria (*Nitrosomonas* and *Nitrosospira*) and Gammaproteobacteria (*Nitrosococcus*) classes (Purkhold et al., 2000), and ammonia-oxidizing archaea (AOA) belonging to the Thaumarchaeota phylum, such as *Nitrosopumilus maritimus* (Könneke et al., 2005) and *Cenarchaeum symbiosum* (Hallam et al., 2006). The discovery of AOA solved the long-standing mystery of the apparently rare ammonia oxidizers in the ocean (Wuchter et al., 2006).

Until recently, NH_3 oxidation was thought to be a two-step process in AOB, with large gaps still remaining in the AOA pathway (Walker et al., 2010; Vajrala et al., 2013; Kozlowski et al., 2016). The first and usually rate-limiting step is the conversion of NH_3 to hydroxylamine (NH_2OH), catalyzed by the ammonia monooxygenase (AMO). The second step was once believed to be the conversion of NH_2OH to NO_2^- by the hydroxylamine oxidoreductase (HAO), but recent studies indicate that NH_2OH is first converted to nitric oxide (NO), and then to NO_2^- (Kozlowski et al., 2016; Caranto and Lancaster, 2017), raising the possibility that NH_3 oxidation in AOA is also a three-step process (Carini et al., 2018). The pathways for the oxidation of NH_2OH to NO and then to NO_2^- must be characterized to fully understand the bioenergetics of NH_3 oxidation in AOB and AOA (Lancaster et al., 2018).

The AMO enzyme is encoded by the *amoABC* operon. The *amoA* gene has been widely used as a molecular marker for studying ammonia oxidizers in the environment (Rotthauwe and Witzel, 1997). The HAO enzyme is a homotrimer and is encoded in the *hao* gene, present in AOB with multiple copies (Arp et al., 2007). The *hao* gene has been little-used as a molecular marker of AOB in marine systems (Lüke et al., 2016; Rasigraf et al., 2017). No homologs of *hao* gene have been identified in the genome from any known AOA, suggesting that AOA probably catalyze NH_2OH oxidation *via* a novel enzyme complex (Vajrala et al., 2013; Kozlowski et al., 2016) or produce a reactive nitroxyl (HNO) intermediate instead of NH_2OH (Walker et al., 2010).

Ammonia oxidizers are important contributors to marine nitrous oxide (N_2O) production (Santoro et al., 2011; Löscher et al., 2012; Trimmer et al., 2016); although the exact metabolic pathways and their relative importance for global N_2O production remain unclear. AOB can produce N_2O by nitrifier denitrification (see section Denitrification) through NO_2^- reduction *via* a NO intermediate (Stein, 2011), as well as a by-product of the nitrification through incomplete NH_2OH oxidation to either HNO or NO (Caranto and Lancaster, 2017) or *via* the enzymatic oxidation of NH_2OH (Caranto et al., 2016). AOA also produce N_2O by pathways that are apparently similar but less well understood (Stieglmeier et al., 2014; Kozlowski et al., 2016).

The NO_2^- oxidation is catalyzed by the nitrite oxidoreductase (NXR), which is present in nitrite-oxidizing bacteria (NOB), a phylogenetically diverse group belonging to Chloroflexi, Nitrospirae, Nitrospinae and several classes of Proteobacteria (Daims et al., 2016). The NXR enzyme is closely related to the membrane-bound nitrate reductases (NAR) (Lücker et al., 2010), and is comprised of three subunits: NxrA, NxrB and NxrC. The *nxrAB* genes, along with the 16S rRNA gene, have been the most used markers for studying NOB in marine environments (e.g., Bristow et al., 2015; Rani et al., 2017). Some marine NOB, such as *Nitrospira*, are mixotrophs and can produce NH_3 from urea, thus sustaining ammonia oxidizers that provide NO_2^- to *Nitrospira* (Koch et al., 2015). NOB of the genus *Nitrospina* have exclusively been found in marine environments (Mincer et al., 2007; Beman et al., 2013; Levipan et al., 2014) and have only two known cultured species to date: *N. gracilis*, isolated from ocean surface waters (Watson and Waterbury, 1971), and *N. watsonii*, isolated from the suboxic zone of the Black Sea (Spieck et al., 2014). *Nitrospina* is the most abundant and globally distributed

marine NOB and has a key role in the oceanic NO_2^- oxidation and C fixation (Pachiadaki et al., 2017).

Comammox bacteria were discovered in 2015 (Daims et al., 2015; van Kessel et al., 2015) and have been classified as members of lineage II within *Nitrospira* (Daims et al., 2015). These organisms have a high affinity for NH_3 and may be well adapted to oligotrophic environments (Kits et al., 2017). A metagenomic survey recently found a relatively high proportion of comammox bacteria in coastal water and sediment samples, whereas they were nearly undetectable in open-ocean samples (Xia et al., 2018). Further research of comammox bacteria is needed in marine environments to assess their contribution to marine nitrification.

Factors affecting nitrification in marine systems

Oxygen, NH_4^+, NO_2^-, light, pH, temperature, and salinity are among the main factors allowing niche differentiation of the main nitrifier groups (Bouskill et al., 2012) and the decoupling of the two steps of nitrification in some marine environments (Heiss and Fulweiler, 2016; Zakem et al., 2018). Nitrifiers require O_2, but they seem to do well in microaerophilic conditions. In this context, it has been observed that NH_3 oxidation and NO_2^- oxidation persist even at nanomolar O_2 levels in OMZs, suggesting that specialist nitrifiers have developed an exceptionally high affinity for O_2 in this habitat (Füssel et al., 2012; Bristow et al., 2016, 2017; Sun et al., 2017). Furthermore, O_2 and NO_2^- might be the primary drivers of niche differentiation of marine NOB species, since OMZ NOB species seem to be more adapted to lower O_2 but higher NO_2^- concentrations than non-OMZ NOB species (Watson and Waterbury, 1971; Sun et al., 2017).

Photoinhibition of marine nitrifiers has been also reported (e.g., Merbt et al., 2012; Pedneault et al., 2015; Peng et al., 2016; Horak et al., 2018), but observations of nitrification and the frequent retrieval of *amoA* genes close to the sea surface (Mincer et al., 2007; Christman et al., 2011; Shiozaki et al., 2016) suggest that this is not universally the case. Thus, light might be an indirect control on nitrification (Zakem et al., 2018), and the base of the euphotic zone might be an optimal location for nitrifiers in stratified water columns (Santoro et al., 2010; Beman et al., 2012; Peng et al., 2016): phytoplankton outcompete slow-growing nitrifiers for NH_4^+ and NO_2^- in the sunlit ocean, but not deeper where light limits phytoplankton (Smith et al., 2014b). Differential photoinhibition has been also proposed as the mechanism that maintains the oceanic primary NO_2^- maximum at the base of the euphotic zone (where high NH_3 oxidation rates and AOA abundance have been found; Newell et al., 2013; Peng et al., 2015) because NOB are more sensitive to light than ammonia oxidizers (Olson, 1981). Additionally, light might be an important factor structuring marine AOA in two distinct ecotypes by depth; the water column group A (WCA) or "shallow" ecotype, with putative adaptive mechanisms to reduce light-induced damage, and the water column group B (WCB) or "deep" ecotype (Luo et al., 2014). Other factors, such as different substrate affinities (Sintes et al., 2013; Smith et al., 2016) or the ability to use organic substrates (Alonso-Sáez et al., 2012; Qin et al., 2014), also influence the vertical distribution of AOA ecotypes.

Elevated temperature may drives decoupling of NH_3 and NO_2^- oxidation, leading to NO_2^- accumulation in some coastal waters (Bristow et al., 2015; Schaefer and Hollibaugh, 2017), and can affect the composition and abundance of AOA communities in several bays (Mosier and Francis, 2008; He et al., 2018). Temperature also seems to be an important factor influencing the diversity of ammonia oxidizers in sponge associations (Cardoso et al., 2013) and deep-sea seep sediments (Dang et al., 2010b). Marine NOB can grow in a broad temperature range and sequences from this group have been recovered from polar environments (Rani et al., 2017) to deep-sea brines with temperatures up to 65°C (Ngugi et al., 2016).

Other factors affecting marine nitrifier communities are site-specific. For example, in deep-sea environments, total C, N and sulfur (S) seem to control the distribution of ammonia oxidizers (Xu et al., 2014; Luo et al., 2015). Moreover, salinity is an important factor driving *amoA* gene diversity in estuaries (e.g., Francis et al., 2003; Bernhard et al., 2005, 2010; Hou et al., 2018). High salinity also seems to affect NOB communities (Oren, 2011; Monteiro et al., 2017), although *Ca.* Nitromaritima RS can thrive over 11% salinity in the Red Sea brines (Luo et al., 2015).

Distribution of nitrifier communities in marine environments

Open oceans. The distribution and activity of ammonia oxidizing communities in the open ocean has been widely studied (**Table 1**). In this NH_4^+-limited environment, AOA are present throughout the water column and dominate over AOB (e.g., Beman et al., 2008; Newell et al., 2011; Pajares et al., 2019), which sometimes go undetected (Mincer et al., 2007; De Corte et al., 2009; Molina et al., 2010). A potential explanation for the marine AOA dominance is their high substrate affinity that could provide a competitive advantage over AOB (Martens-Habbena et al., 2009).

There is not a clear pattern of depth distribution of both AOB and AOA in the open ocean. For example, AOA are mainly present in the euphotic layer and AOB are confined to higher depths in the Sargasso Sea, the North Pacific Ocean, the Arctic Ocean and the Gulf of California (Beman et al., 2012; Newell et al., 2013; Shiozaki et al., 2016), while AOA are predominantly distributed below the euphotic zone in the central and subtropical Pacific Ocean (Mincer et al., 2007; Church et al., 2010). Moreover, AOA form vertical and latitudinal gradients throughout the North Atlantic, where their abundance and diversity decrease in meso- and bathypelagic waters from the north toward the equator (Agogué et al., 2008).

Abundant and active ammonia oxidizers have been found in OMZs (Newell et al., 2011; Peng et al., 2015, 2016), such as those in the Arabian Sea and the Eastern Tropical North Pacific (ETNP), where ammonia oxidizers and anammox bacteria have different vertical distributions in the anoxic layer (Pitcher et al., 2011a; Pajares et al., 2019), the Eastern Tropical South Pacific (ETSP), where both AOA and AOB exhibit a strong *amoA* expression in the upper OMZ (Lam et al., 2009), and the Baltic Sea, where the high abundance of AOA suggests a tolerance of this group to anoxic and sulfidic waters (Berg et al., 2015).

The two ecotypes of AOA are distributed at different depths in the open ocean (Francis et al., 2005; Luo et al., 2014). The WCA

is typically more abundant in the sunlit ocean, while the WCB dominates the meso- and bathypelagic, where light is absent and the NH_4^+ flux is very low but the availability of other growth substrates (e.g., urea) is high (Sintes et al., 2013; Santoro et al., 2017). This distribution of AOA ecotypes has been found in different marine systems such as OMZs (Beman et al., 2008; Molina et al., 2010), coastal upwelling region (Santoro et al., 2010), warmer waters with P deficit (De Corte et al., 2009), and colder waters (Shiozaki et al., 2016; Smith et al., 2016). WCA abundance has been associated with the highest nitrification rates, suggesting that this ecotype is responsible for most of the NH_3 oxidation in the ocean (Santoro et al., 2017).

In contrast with ammonia oxidizers, NOB distribution is less understood in marine environments. *Nitrococcus*, with only one species known to date (*N. mobilis*) (Watson and Waterbury, 1971), can dominate in certain marine areas such as the Namibian OMZ (Füssel et al., 2012, 2017). *Nitrospina*-like NOB have been found in abundance in different areas of the global ocean, such as at open-ocean benchmark research sites as the Hawaii Ocean Time-series (HOT) (DeLong et al., 2006) and San Pedro Ocean Time-series (SPOT) (Beman et al., 2010), but exhibits a preference for mesopelagic waters (Mincer et al., 2007), sediments (Reyes et al., 2017) and OMZs (Füssel et al., 2012; Levipan et al., 2014; Ganesh et al., 2015; Lüke et al., 2016). Two novel uncultured *Nitrospina*-like species have been recently identified in high abundance in OMZs (Sun et al., 2019), which is consistent with the detection of higher NO_2^- oxidation rates in OMZs than in oxic seawaters and suggests novel adaptations of specialist NOB to anoxic environments. Furthermore, it was hypothesized that NOB in OMZs might benefit from utilizing alternative terminal electron acceptors for NO_2^- oxidation, such as iodate, manganese or Fe (Lam and Kuypers, 2011; Casciotti and Buchwald, 2012). Their significance in OMZs, specifically in counteracting N loss through denitrification and anammox, has been recognized in recent years (Beman et al., 2013; Buchwald et al., 2015; Bristow et al., 2017).

Estuaries and coastal environments. The diversity of ammonia oxidizers in estuaries might be greater than that in the adjacent open oceans due to nutrient discharge from rivers (Cao et al., 2011; He et al., 2018). Both AOA and AOB are frequently found together in estuarine and coastal sediments, although the AOA community is usually more diverse than AOB community (Beman and Francis, 2006; Jin et al., 2011; Zheng et al., 2014; Zhang Y. et al., 2014). However, the dominance of one group over the other is unclear. In some estuaries and coasts, AOA form the most abundant ammonia oxidizer community (e.g., Caffrey et al., 2007; Lipsewers et al., 2014; Tait et al., 2014; Urakawa et al., 2014; Zhang Y. et al., 2014), while in others they are less abundant than or equal to AOB (e.g., Zheng et al., 2014; Fan et al., 2015b; Li et al., 2015; Smith J. M. et al., 2015). The salinity gradient is one of the main factors controlling the distribution and activity of nitrifier communities in estuarine sediments, where AOA and AOB seem to occupy different niches (**Table 1**). AOB are usually more abundant where salinity and N content are higher, while AOA dominates in the part exhibiting low salinity and N content (Mosier and Francis, 2008). Further, AOA belonging to "sediment" and "marine" clades (*Nitrosopumilus*-like sequences) are more abundant in the mouth, whereas AOA belonging to the "low salinity" (*Nitrosoarchaeum*-like sequences) and "soil" (group 1.1b) clades are more abundant in the head of many estuaries (e.g., Francis et al., 2003; Beman and Francis, 2006; Mosier and Francis, 2008; Bernhard et al., 2010). Similarly, AOB sequences belonging to the *Nitrosospira*-like cluster have mostly been obtained at high salinities, while the *Nitrosomonas*-like cluster is dominant at low salinities (Francis et al., 2003; Bernhard et al., 2005).

The structure of AOA populations follows different patterns in coastal waters. For instance, WCA organisms seem to be distributed at all depths, whereas WCB organisms are confined to low-O_2 and low-chlorophyll deeper waters in the Pacific coasts (Smith et al., 2014a; Bertagnolli and Ulloa, 2017). Additionally, AOA populations fluctuate seasonally, with abundance peaks during winter in the coastal Arctic and North Sea (Christman et al., 2011; Pitcher et al., 2011b), whereas in the Chilean coast, WCB organisms are abundant during spring and summer and non-detectable during winter (Bertagnolli and Ulloa, 2017).

NOB diversity in estuaries is also strongly influenced by salinity. For instance, distinctive NOB phylotypes have been detected along a salinity gradient in estuarine sediments, where NOB increase their abundance as salinity decreases (Monteiro et al., 2017). Additionally, salinity and NO_2^- flux may be major factors causing niche differentiation of NOB groups in estuarine waters, where *Nitrospina* could be more adapted to low-nutrients and high-salinity conditions, while *Nitrospira* could be well adapted to eutrophic estuarine conditions (Hou et al., 2018). Finally, NH_3 and NO_2^- oxidation are not always coupled in coastal waters (Heiss and Fulweiler, 2016), which may be due to a decoupling between AOA and *Nitrospina* populations (Bristow et al., 2015).

Deep-sea environments. Deep-sea sediments and hydrothermal vents are sites of active nitrification that harbor diverse ammonia-oxidizing prokaryotes (**Table 1**; Nakagawa et al., 2007; Dang et al., 2009a; Baker et al., 2012). In these systems, AOA are much more diverse but less abundant than AOB (Cao et al., 2012; Xu et al., 2014; Luo et al., 2015), although several exceptions have been found (Dang et al., 2010b; Nunoura et al., 2013). NOB community has been understudied in deep-sea environments, where they seem to be very abundant (Baker et al., 2013; Nunoura et al., 2013; Ngugi et al., 2016; Tully and Heidelberg, 2016). Further, distinctive distribution of NOB has been found, with *Nitrospina* more abundant in the bathyal waters and *Nitrospira* more abundant in the hadal waters (Nunoura et al., 2015).

Symbiosis with coral reefs and other marine organisms. The few studies of the nitrifying ecology in coral reefs suggest that AOA may be the main contributors to N cycling in these systems (Beman et al., 2007), with *N. maritimus* as an important player that oxidizes NH_3 during daytime when the conditions in coral mucus are oxic (Siboni et al., 2008). However, AOB seem to dominate nitrifier communities in other coral species (Yang et al., 2013). Further research in this direction would help understand the importance of both ammonia oxidizer groups in a variety of coral species.

Ammonia oxidizers have also been studied in symbiosis with other marine organisms. The first genome assembly of a marine AOA was generated from *C. symbiosum*, which accounts for 65% of microorganisms associated with the sponge *Axinella mexicana* (Preston et al., 1996; Hallam et al., 2006). However, *Nitrosospira* and *Nitrosopumilus*-related AOA seem to be the major drivers of nitrification in different types of sponges (Mohamed et al., 2010; Radax et al., 2012; Zhang F. et al., 2014). In addition, AOA play an important nitrification role within the tissue of colonial ascidians (Martínez-García et al., 2008).

Dissimilatory Nitrate Reduction to Ammonia (DNRA)

Respiratory ammonification or DNRA is an anaerobic process in which NO_3^- is reduced to NO_2^- and then to NH_4^+, though the reaction may begin with NO_2^- directly. DNRA is mainly a heterotrophic process, but it can also be an autotrophic process driven by inorganic compounds such as sulfide (S^{-2}), elemental S, or Fe^{+2} (Robertson et al., 2016; Slobodkina et al., 2017).

NO_3^- reduction is a major source of NO_2^- for other N-cycling processes, including aerobic NO_2^- oxidation and anammox, and in DNRA occurs in the same way as in denitrification. It is mainly catalyzed by either the NarGHI complex, present in a wide variety of microorganisms, or the periplasmic nitrate reductase complex (NapAB), present mainly in Gram-negative bacteria (Moreno-Vivián et al., 1999; Simon and Klotz, 2013). The active sites of both complexes are encoded in *narG* and *napA* genes, which have been used as biomarkers for the marine microorganisms involved in NO_3^- reduction (e.g., Smith et al., 2007; Lam et al., 2011).

The reduction of NO_2^- to NH_4^+ in the heterotrophic DNRA is catalyzed by the cytochrome C nitrite reductase (ccNIR), encoded in the *nrfA* gene, which is frequently used as a biomarker for the DNRA process (e.g., Papaspyrou et al., 2014; Welsh et al., 2014). The reduction of NO_2^- to NH_4^+ in the chemolithotrophic DNRA is mainly catalyzed by the octaheme tetrathionate reductase (Otr) (Atkinson et al., 2007) or the octaheme cytochrome C nitrite reductase (Onr) (Tikhonova et al., 2006).

A broad diversity of microorganisms is capable of DNRA, mainly prokaryotic organisms belonging to Proteobacteria, Firmicutes, Verrucomicrobia, Planctomycetes, Acidobacteria, Chloroflexi, and Chlorobia (Tiedje, 1988; Welsh et al., 2014). Marine eukaryotes capable of DNRA include diatoms, which use DNRA to enter a resting stage for long-term survival in dark anoxic sediments (Kamp et al., 2011), and fungi such as *Aspergillus terreus* isolated from the Arabian Sea OMZ (Stief et al., 2014). Evidence of chemolithotrophic DNRA in marine sediments has been found in *Beggiatoa* (Preisler et al., 2007), as well as in *Thermosulfurimonas dismutans* and *Dissulfuribacter thermophilus*, thermophilic anaerobic bacteria isolated from deep-sea hydrothermal vents (Slobodkina et al., 2017).

Factors affecting DNRA in marine systems

DNRA produces NH_4^+ without the release of N_2 and contributes to nitrification and anammox. Therefore, understanding the mechanisms controlling the DNRA community and its interactions with other N-cycling communities is critical for understanding the fate of N in marine systems.

DNRA and denitrification compete for NO_3^- and there are several factors favoring DNRA over denitrification, such as high S^{-2} concentrations and C:NO_3^- ratio, elevated temperatures, salinity and anoxic conditions (e.g., Dong et al., 2011; Song et al., 2014; Yin et al., 2017). Although DNRA has a lower energetic yield than denitrification, it can accept a greater number of electrons per NO_3^- molecule (eight, compared to five for denitrification). For this reason, DNRA may be energetically favored over denitrification in anoxic environments where NO_3^- is limiting and electron donors (organic C or S^{-2}) are in excess (Dong et al., 2011; Kraft et al., 2014). It has been suggested that DNRA is not affected by NH_4^+ (Tiedje, 1988) and NO_2^- (van den Berg et al., 2017), but it has been demonstrated that NH_4^+ and NO_2^- concentrations are positively correlated with DNRA rates in estuaries (Song et al., 2014; Lisa et al., 2015; Yin et al., 2017). Salinity seems to be another factor affecting DNRA, although there is not a clear pattern. In some estuaries DNRA rates increase with increasing salinity (Gardner et al., 2006; Giblin et al., 2010; Lisa et al., 2015), while in others DNRA rates decrease (Dong et al., 2009). Finally, elevated temperatures favor DNRA rates; therefore, DNRA may be an important pathway for NO_3^- reduction in (sub)tropical estuaries (Gardner and McCarthy, 2009; Dong et al., 2011; Yin et al., 2017).

Distribution of DNRA communities in marine environments

Since DNRA is an anaerobic process, marine DNRA communities are mostly restricted to anoxic environments such as sediments and OMZs (**Table 1**). However, there are relatively few studies on DNRA communities in those marine systems compared to the number of studies on microbes involved in other N-cycling processes.

Open oceans and deep-sea environments. Only a few studies on DNRA distribution have been conducted in open oceans, most of them in OMZs. In the Arabian sea OMZ, DNRA is coupled with anammox (Jensen et al., 2011), and is carried out by microorganisms with divergent *nrfA* genes (Lüke et al., 2016). In Baltic Sea sediments *nrfA* has been found in lower abundance than genes involved in denitrification, possibly due to the combination of low-sulfide, oligotrophic and hyposaline conditions of this environment (Rasigraf et al., 2017; Reyes et al., 2017). DNRA has also been detected in the ETNP and ETSP OMZs, where it may supply most of the NH_4^+ needed for anammox (Lam et al., 2009; Pajares et al., 2019). However, several studies have reported low or undetectable *nrfA* genes and low DNRA rates in the ETSP, suggesting that this process may be sporadic (Kalvelage et al., 2013; Schunck et al., 2013) or that anammox bacteria could perform both DNRA and anammox producing their own NH_4^+ from NO_3^- (Kartal et al., 2007; De Brabandere et al., 2014).

DNRA communities have also been found in deep-sea sediments, where microbes involved in DNRA, nitrification and anammox are more abundant than in shallow sediments (Yu et al., 2018). More studies are needed to confirm the importance of DNRA in deep-sea environments.

Estuarine zones. Diversity and abundance of the *nrfA* gene in estuaries are high and often change along salinity and NO_3^- gradients (e.g., Papaspyrou et al., 2014; Song et al., 2014; Smith C. J. et al., 2015). There are exceptions such as in the Yellow River estuary, where the abundance and activity of DNRA communities are not affected by either type of gradient (Bu et al., 2017). Additionally, DNRA communities from estuarine sediments are site-specific and could vary significantly at a small spatial scale (Decleyre et al., 2015; Zheng et al., 2016). For example, in the well-studied Colne estuary (United Kingdom), DNRA communities embedded in deeper anoxic sediments are more homogeneous compared to those in the surface (Takeuchi, 2006). Furthermore, *in situ* rates of denitrification and DNRA along with gene markers for nitrate reduction (*narG*), denitrification (*nirS*), and DNRA (*nrfA*) decrease toward the mouth of that estuary where the NO_3^- concentration is lower, while denitrification potential also decrease but DNRA potential increase (Smith et al., 2007; Dong et al., 2009; Papaspyrou et al., 2014; Smith C. J. et al., 2015), indicating that DNRA microorganisms are more competitive than denitrifiers when the ratio of electron donors to electron acceptors increase, which stimulates DNRA relative to denitrification. Finally, higher *nrfA* abundance and DNRA rates have been found in estuarine sediments richer in organic C and S^{-2} (Song et al., 2014; Yin et al., 2017).

N-Loss Processes

The oceanic N budget balance leans more toward higher losses (between ∼275–481 Tg N yr^{-1}) than inputs (between ∼265–294 Tg N yr^{-1}) (Codispoti et al., 2001; Codispoti, 2007; Gruber and Galloway, 2008; Voss et al., 2013). The N release from the ocean is mainly caused by denitrification and anammox in a theoretical 71:29 ratio, assuming that anammox consumes all NH_4^+ produced from mineralization of C and N in a 106:16 ratio coupled to denitrification (Dalsgaard et al., 2012). The most important factor over marine N loss is O_2 given that denitrification and anammox occur in environments where O_2 is nearly or fully depleted, such as OMZs and sediments, which are responsible for 30–50% and 50–70% of N loss, respectively (Codispoti et al., 2001; Devol, 2015; Na et al., 2018). The interaction of denitrification and anammox with other N processes also affects marine N loss. As discussed below, DNRA and denitrification coexist in anoxic environments, but DNRA may be favored in environments with low NO_3^- and high organic C (Kraft et al., 2014). DNRA interaction with anammox could enhance N loss, because DNRA feeds anammox by increasing NH_4^+ concentrations (Jensen et al., 2011). Nitrate/nitrite-dependent anaerobic methane oxidation (N-damo) has recently identified as a N-loss process (Padilla et al., 2016), but its contribution to the global marine N loss has not yet been investigated.

Among dissolved gaseous N compounds, marine N_2O has caught the most attention of the scientific community in the last years (Bange et al., 2010; Martinez-Rey et al., 2015), because it is a potent greenhouse gas and an ozone-depleting agent that is mainly produced by NH_3 oxidation and denitrification (Freing et al., 2012). Estimates of global oceanic N_2O emissions range between 3.8 Tg N yr^{-1} (Ciais et al., 2013) and 4.3 Tg N yr^{-1} (Battaglia and Joos, 2018), ∼35% of total N_2O natural emissions (Syakila and Kroeze, 2011). The highest oceanic N_2O concentrations and fluxes occur in coastal upwelling ecosystems (Nevison et al., 2004; Arévalo-Martínez et al., 2015) and OMZs (e.g., Naqvi and Noronha, 1991; Kock et al., 2016; Bourbonnais et al., 2017; Casciotti et al., 2018), in which it is produced near the oxycline where a decoupling between N_2O production from both NH_3 oxidation and denitrification and consumption by denitrification occurs (Farías et al., 2009; Dalsgaard et al., 2014; Babbin et al., 2015; Ji et al., 2015), as the latter process is less O_2 tolerant.

Denitrification

Denitrification is a respiratory pathway performed by diverse facultative anaerobic microorganisms in which NO_3^- is respired to NO_2^- (discussed in the DNRA section), followed by stepwise reductions to NO, N_2O, and N_2 (Zumft, 1997). Denitrification is a modular pathway, in which a microorganism may not always possess the full set of enzymes and thus perform only a subset of steps within the pathway (Graf et al., 2014).

Two isofunctional but structurally divergent periplasmic enzymes catalyze the reduction of NO_2^- to NO (Simon and Klotz, 2013): a Cu-containing nitrite reductase (encoded by *nirK*) and a haem-containing cd_1 nitrite reductase (encoded by *nirS*), which are thought to be mutually exclusive in the genome of denitrifying organisms (Jones et al., 2008), although some exceptions have been found (Graf et al., 2014). Because this is the first committed step of the pathway to a N gaseous product, *nir* genes are the most widely used markers for denitrifiers (e.g., Braker et al., 2000; Mosier and Francis, 2010; Pajares et al., 2019). The *nir* genes are present in many other microorganisms, including anammox bacteria, nitrite and methane-oxidizing bacteria, AOA and AOB (Kuypers et al., 2018). Moreover, several studies have shown evidence of niche differentiation between *nirK* and *nirS* communities (Jones and Hallin, 2010; Wittorf et al., 2016; Pajares et al., 2017). Furthermore, *nirS*-denitrifiers seem to have a complete denitrification pathway (including *nor* and *nos* genes); thus, they are more likely to completely reduce NO_2^- to N_2 (Graf et al., 2014).

The conversion of NO to N_2O is carried out mainly by the nitric oxide reductases cNOR (a cytochrome c-dependent complex) or qNOR (a quinol-dependent complex), whose active sites are encoded by two variants of the same gene (*cnorB* and *qnorB*, respectively) (Simon and Klotz, 2013). The cNOR has also been found in AOB (Casciotti and Ward, 2005), while qNOR has also been found in N-damo and non-denitrifying microorganisms, where it may play a detoxifying role (Jones et al., 2008; Wu et al., 2011). Both *qnorB* and *cnorB* have been little used as biomarkers for marine NO-reducing denitrifiers (Braker and Tiedje, 2003; Ganesh et al., 2015).

The final step in the denitrification pathway is the reduction of N_2O to N_2. It is catalyzed by the nitrous oxide reductase (NOS), which is encoded in the *nosZ* gene and is frequently used as a biomarker of N_2O-reducing denitrifiers in marine systems (e.g., Bowles et al., 2012; Wittorf et al., 2016). There are two phylogenetically distinct *nosZ* clades: clade I includes organisms with a complete denitrification pathway, whereas clade

II includes organisms that frequently lack other denitrification genes (Jones et al., 2013).

Denitrification is mainly a heterotrophic process, although autotrophic denitrifiers, which use H_2 or S compounds as electron donors, have been found in many marine environments, including OMZs (Lam and Kuypers, 2011, and references therein), hydrothermal vent sediments and microbial mats (e.g., Shao et al., 2011; Bowles et al., 2012).

Finally, a partial denitrification pathway has been reported in marine AOA and AOB. In the called "nitrifier denitrification," NO_2^- is reduced to N_2O *via* a NO intermediate under suboxic or anoxic conditions (Frame and Casciotti, 2010; Zhu et al., 2013). Nitrifier denitrification was originally thought to be restricted within some AOB harboring Nir and Nor enzymes (Stein, 2011). However, the observation of high N_2O production rates under low O_2 concentrations for *N. maritimus* suggests that marine AOA might play an important role in N_2O production *via* this pathway (Löscher et al., 2012) or *via* a hybrid formation (Kozlowski et al., 2016). Nitrifier denitrification has been observed in the lower euphotic zone of the open ocean (Wilson et al., 2014) and OMZs (Löscher et al., 2012; Bourbonnais et al., 2017).

Factors affecting denitrification in marine systems

Denitrification is limited to environments where O_2 is nearly fully depleted. It has been reported that *nirS, norB* and *nosZ* transcripts strongly decrease in O_2 concentrations > 200 nM (Dalsgaard et al., 2014), and *nirS* is rarely present in well-oxygenated waters (Jayakumar et al., 2004; Ward et al., 2009). Furthermore, O_2 availability is associated with the habitat partitioning of NO_2^- and N_2O reducers, with *nirS*- and *nosZI*-type denitrifiers prevailing under lower O_2 regimes (Kim et al., 2011; Wittorf et al., 2016).

Heterotrophic denitrifiers depend on a supply of organic matter, and incubation experiments in OMZs suggest that organic C is a major driver of denitrification, which might be linked to the episodic supply of organic substrates from productive surface waters (Ward et al., 2008; Babbin et al., 2014). The composition and stoichiometry of the source organic matter may also determine the dominant N-loss process: fresh organic matter with higher C:N ratio stimulates denitrification over anammox because denitrification uses organic matter directly while anammox uses NH_4^+ from organic matter degradation (Babbin et al., 2014; Chang et al., 2014). Furthermore, N_2O and N_2 production associated with denitrifying communities have been found in particles, whereas other N processes are more associated with free-living communities in OMZs (Ganesh et al., 2015; Fuchsman et al., 2017). The structure and abundance of denitrifiers in OMZs is also correlated with NO_3^- and NO_2^- concentrations (Liu et al., 2003; Castro-Gonzalez et al., 2005; Jayakumar and Ward, 2013). Additionally, chemolithotrophic denitrification may be responsible for N_2 production in OMZs where hydrogen sulfide (H_2S) accumulates (Galán et al., 2014).

The input and type of organic matter and salinity are among the key factors controlling denitrification rates and denitrifier community distribution in estuaries (e.g., Mosier and Francis, 2010; Eyre et al., 2013; Francis et al., 2013; Zhang Y. et al., 2014; Lee and Francis, 2017). Since NirK and NosZ require Cu, it could represent a regulating factor in denitrification and the production of N_2O in marine environments (Granger and Ward, 2003). However, it has been observed that increasing concentrations of Cu decrease the abundance and diversity of denitrifiers and inhibit denitrification rates in estuarine sediments (Magalhães et al., 2011). As mentioned before, denitrification and DNRA compete for NO_3^-, and factors such as low S^{-2} concentrations (which inhibit the last two steps of denitrification), cold temperatures, and a low C:NO_3^- ratio favor denitrification over DNRA (Burgin and Hamilton, 2007; Smith C. J. et al., 2015).

Distribution of denitrifier communities in marine environments

Although denitrifying microorganisms can be found in any marine environment, denitrification is typically restricted to suboxic or anoxic environments such as OMZs and sediments (**Table 1**).

Open oceans and deep-sea environments. OMZs are considered one of the major oceanic sites of denitrification. For example, denitrification is the dominant N-loss pathway in the Arabian Sea OMZ (Ward et al., 2009), where denitrifiers dominate over anammox bacteria (Jayakumar et al., 2009; Sokoll et al., 2012); although a recent report has found higher abundance of anammox genes over denitrifying genes in this OMZ (Bandekar et al., 2018). Depth distributions of *nir* genes follow the same pattern in the Arabian Sea, ETNP and ETSP, where they are associated with the secondary NO_2^- maximum in oxygen-depleted waters (Bandekar et al., 2018; Pajares et al., 2019). However, the denitrifier community composition of these sites seems to be different (Jayakumar and Ward, 2013; Bandekar et al., 2018). In the ETNP, *narG* belonging to SAR11 clades is the most abundant denitrifying gene (Tsementzi et al., 2016), while *nirK* dominates over *nirS* (Fuchsman et al., 2017). In the Black Sea, *nirK*-based communities vary with depth, while the composition of both *nirK* and *nirS* genes changes at the bottom of this suboxic zone (Oakley et al., 2007). Great genomic potential for full denitrification to N_2 but less genomic potential for anammox and DNRA have been found in Baltic Sea sediments (Rasigraf et al., 2017; Reyes et al., 2017). Additionally, the composition of *nirS*-based communities is site-specific in this environment and varies along biogeochemical gradients in the water column, while it is uniform in the sediment (Falk et al., 2006; Hannig et al., 2006). Finally, the *nosZ*-based communities have a strong biogeographical separation, thus the communities from surface ocean waters differ from those in OMZs (Jayakumar et al., 2018).

Few studies of denitrifier communities have been conducted in deep-sea sediments and hydrothermal vents, where chemolithotrophic denitrification seems to be an important process given the high concentration of reduced S species in such environments (Shao et al., 2011; Bowles et al., 2012). In addition, *nirS* sequences have been retrieved from these systems (Bourbonnais et al., 2014), where *nirK*-type denitrifiers were undetected (Tamegai et al., 2007).

Estuaries and coastal environments. Denitrification is often the major process driving N removal from coastal and estuarine

environments (Damashek and Francis, 2018, and references therein). Sediments provide ideal conditions for this process, due to the narrow spatial scale for diffusion across redox boundaries. Therefore, most studies have documented the diversity and activity of denitrifiers in estuary sediments (e.g., Abell et al., 2010; Magalhães et al., 2011; Wang et al., 2014; Smith J. M. et al., 2015), with a few of them in estuary waters (e.g., Santoro et al., 2006; Zhang Y. et al., 2014; Smith C. J. et al., 2015). Denitrifiers often change along the estuarine salinity gradient, with distinct communities in fresh and marine regions (e.g., Abell et al., 2013; Francis et al., 2013; Lee and Francis, 2017). For instance, in the San Francisco Bay estuary, the abundance of *nirK* is higher in the riverine zone, whereas *nirS* is more abundant in marine zones (Mosier and Francis, 2010). Additionally, denitrification rates and the abundance of nitrate and nitrite genes usually decline from the estuary head toward the mouth, where NO_3^- concentrations are lower (Smith et al., 2007; Dong et al., 2009).

Other environments. Denitrification also occurs in other niches outside anoxic sediments and OMZs. For example, the low-oxygen environment within *Trichodesmium* colonies allows the growth of active denitrifiers harboring *nosZ* genes, representing a potential sink for N_2O within oceanic surface waters (Wyman et al., 2013; Coates and Wyman, 2017). Diverse bacteria harboring *nir* genes have been also found in corals and sponges (Hoffmann et al., 2009; Yang et al., 2013). Additionally, sinking copepod carcasses have anoxic interiors that support the expression of *nirS* genes, representing hotspots of pelagic denitrification (Glud et al., 2015). Finally, certain benthic foraminifera are capable of accumulating and respiring NO_3^- through denitrification (Risgaard-Petersen et al., 2006; Pina-Ochoa et al., 2010), which is their preferred respiration pathway in OMZs, contributing substantially to total benthic NO_3^- loss in these environments (Glock et al., 2013, 2019).

Nitrate/Nitrite-Dependent Anaerobic Methane Oxidation (N-Damo)

Anaerobic CH_4 oxidation coupled with denitrification (N-damo) was discovered in 2006 and constitutes a unique link between the C and N cycles (Raghoebarsing et al., 2006).

The N-damo process is carried out by ANME archaea and NC10 bacteria. *Ca.* Methanoperedens nitroreducens (ANME-2d) is one of the microorganisms capable of coupling the anaerobic CH_4 oxidation to NO_3^- reduction to NO_2^- (Haroon et al., 2013), while *Ca.* Methylomirabilis oxyfera (a member of the NC10 phylum) is capable of coupling the anaerobic CH_4 oxidation to NO_2^- reduction to N_2 without the presence of ANME archaea (Ettwig et al., 2010). The metabolism of *Ca.* M. nitroreducens includes genes related to reverse methanogenesis (Haroon et al., 2013; Timmers et al., 2017), such as the methyl coenzyme-M reductase gene (*mcrA*), which has been recently used as a biomarker for methanogens and ANME archaea in marine sediments (Vaksmaa et al., 2017).

The metabolism of *Ca.* M. oxyfera is also complex and unusual, because despite being considered an anaerobic microorganism, it is able to oxidize CH_4 using enzymes found in aerobic methanotrophs (Ettwig et al., 2010) such as the particulate methane-monooxygenase (pMMO), encoded in the *pmoA* gene, which has been used as a biomarker of N-damo bacteria in marine systems (e.g., Chen et al., 2016; Padilla et al., 2016). Metagenomic evidence suggests that *Ca.* M. oxyfera possesses an "intra-aerobic" metabolism consisting of an intracellular production of O_2 by dismutating NO into O_2 and N_2 (Ettwig et al., 2010), although this is yet to be further proven. Its genome also encodes NirS and qNOR, which may participate in detoxifying processes (Wu et al., 2011).

Factors affecting N-damo and its distribution in marine systems

The N-damo process has just begun to be studied, and only a few works on these microorganisms in marine environments are available (**Table 1**). Most of these works has focused on NC10 bacteria and thus information on N-damo archaea is very scarce. The *mcrA* gene and *nar* transcripts affiliated to *M. nitroreducens*-like archaea were recently retrieved from the North Sea sediments (Vaksmaa et al., 2017) and the ETNP OMZ (Thamdrup et al., 2019), respectively, revealing that ANME-2d archaea have niches in marine ecosystems and their roles need to be further explored.

N-damo has been detected in OMZs, which represent a niche for NC10 bacteria (Padilla et al., 2016; Chronopoulou et al., 2017). For example, in the ETNP OMZ, active NC10 bacteria are abundant in the anoxic zone with high NO_2^- and CH_4 concentrations, suggesting that anaerobic NH_4^+ oxidation is coupled to NO_3^- reduction and denitrification (Padilla et al., 2016; Thamdrup et al., 2019). *M. oxyfera*-like bacteria have also been detected in estuarine and coastal sediments, where they show great diversity and a depth-specific distribution influenced by redox potential, water content and total organic C (Li-dong et al., 2014; Zhang et al., 2018). Moreover, the activity of this community in coastal sediments vary seasonally and spatially and seem to be highly influenced by NO_3^- (Shen et al., 2016; Wang et al., 2017), NH_4^+, NO_2^- (Chen et al., 2014, 2015b) and salinity (Chen et al., 2015a; Shen et al., 2016).

The importance of N-damo microorganisms in the C and N cycles, in addition to the small number of studies on their distribution, clearly warrant further study to ascertain the drivers of these communities in different marine ecosystems.

Anammox

Anammox consists in the conversion of NH_4^+ and NO_2^- to N_2 in the absence of O_2. In this process, the initial NO_2^- reduction to NO is believed to be catalyzed by NirS, which has been confirmed in the genomes of *Ca.* Kuenenia stuttgartiensis (Strous et al., 2006) and *Ca.* Scalindua (van de Vossenberg et al., 2008). The production of N_2H_4 from NH_4^+ and NO is catalyzed by the hydrazine synthase (HZS). The N_2H_4 is subsequently oxidized to N_2 by the hydrazine dehydrogenase (HDH), also known as hydrazine oxidase (HZO) (Jetten et al., 2009; Kartal et al., 2011; Simon and Klotz, 2013). Various functional genes have been used as anammox

biomarkers in marine systems: *Scalindua*-like *nirS*, coding for a NirS specific to *Ca.* Scalindua, the dominant anammox bacteria in marine OMZs (Lam et al., 2009); *hzoAB* (Hirsch et al., 2011; Lisa et al., 2014), coding for part of the HDH and with numerous divergent copies in a number of anammox bacteria (Strous et al., 2006); and *hzsA*, coding for part of the HZS, which has been suggested as the most suitable biomarker for the process (Harhangi et al., 2012; Han et al., 2017).

Until now, 10 *Candidatus* species belonging to five genera have been reported as responsible for anammox, all of them within a deep, monophyletic branch in the order Planctomycetales: Kuenenia, Anammoxoglobus and Jettenia with one species each, Brocadia with three species, and Scalindua with four (Kartal et al., 2012; van de Vossenberg et al., 2013). Anammox bacteria are slow-growing anaerobic autotrophs with great affinity for NO_2^- and NH_4^+ (Jetten et al., 2009) that possess a unique capability of producing and converting N_2H_4 in a ladderane lipid membrane called anammoxosome (Kartal et al., 2012).

Anammox coupled to the reduction of sulfate (Sulfammox) and Fe^{+3} (Feammox) has been recently reported in coastal sediments, where both processes may promote significant N losses (Rios-Del Toro et al., 2018). Further studies are required to elucidate the key microbial organisms and mechanisms involved in N_2 production by Sulfammox and Feammox.

Factors affecting anammox in marine systems

Although the presence of anammox bacteria may not be indicative of high anammox activity, several studies have shown that anammox bacterial abundance correlates with anammox rates in marine environments (e.g., Hou et al., 2013; Bale et al., 2014; Lisa et al., 2014). In general, anammox activity is mainly regulated by O_2 and inorganic N concentrations and seems to be coupled with the NO_2^- liberated during aerobic NH_4^+ oxidation (Lam et al., 2007) and NO_3^- reduction (Thamdrup and Dalsgaard, 2002), and the NH_4^+ liberated during denitrification (Dalsgaard et al., 2003) and DNRA (Jensen et al., 2011). Despite being obligated anaerobes active only at O_2 concentrations below 2 μM, anammox bacteria are resistant to O_2 exposure; nevertheless, the process is inhibited at high O_2 concentrations (Jetten et al., 2009). For example, studies have shown that O_2 and NO_2^- co-limit the distribution of anammox bacteria in OMZs (Dalsgaard et al., 2003; Lam et al., 2007; Pitcher et al., 2011a; Kong et al., 2013), although NH_4^+ appears to limit the process in these systems (Lam and Kuypers, 2011). Furthermore, the availability of inorganic N regulates anammox activity in coastal and estuarine sediments (e.g., Trimmer et al., 2005; Nicholls and Trimmer, 2009; Teixeira et al., 2016) in which the fluctuating availability of O_2, NO_3^- and NO_2^- typically favors denitrifying microorganisms over anammox bacteria (Risgaard-Petersen et al., 2005).

In many marine environments anammox is highly dependent on salinity (Rich et al., 2008; Dale et al., 2009; Sonthiphand et al., 2014), temperature (Shehzad et al., 2016; Qian et al., 2018), but mostly on organic matter content (see Section Factors affecting denitrification in marine systems; e.g., Trimmer and Engström, 2011; Babbin et al., 2014). For example, recent studies have demonstrated that organic N substrates could support anammox in OMZs (Babbin et al., 2017; Ganesh et al., 2018), particularly in productive shelf waters (Kalvelage et al., 2013). The contribution of anammox to N_2 loss in sediments seems to be higher at greater water depths where mineralization rates are lower and, therefore, denitrification too. However, anammox rates tend to decrease in deeper sediments because is limited by the NH_4^+ availability (Thamdrup, 2012, and references therein). Conversely, high organic C concentrations in shallow sediments usually stimulate denitrification while suppressing anammox because of the competition for NO_2^- (Nicholls and Trimmer, 2009; Brin et al., 2014). Nevertheless, a number of studies have found positive correlations between organic C content and anammox rates in marine sediments caused by high production of NH_4^+ or NO_2^- from remineralization and nitrification (Trimmer et al., 2003; Hou et al., 2013; Lisa et al., 2015). These contradictions show that understanding the relationship between organic C content and anammox is still an open question.

Distribution of anammox bacteria in marine environments

Anammox bacteria are present and active in a wide range of oxygen-depleted marine environments (**Table 1**) such as the OMZs (e.g., Jensen et al., 2011; Rich et al., 2018), eutrophic bays (e.g., Dang et al., 2010a; Lisa et al., 2014), estuarine sediments (e.g., Trimmer et al., 2005; Li et al., 2011), fjord sediments (Risgaard-Petersen et al., 2004; Brandsma et al., 2011), Arctic sediments (Rysgaard et al., 2004), deep-sea sediments (Hong et al., 2011a; Shao et al., 2014), and hydrothermal vents (Byrne et al., 2009). Below, we summarize the main findings from many studies on the distribution of anammox bacteria in representative marine environments.

Open oceans. OMZs are ideal environments for the growth of anammox bacteria. These bacteria are found in different OMZs such as those in the Black Sea (Kuypers et al., 2003), Golfo Dulce (Dalsgaard et al., 2003), ETNP (Rush et al., 2012; Kong et al., 2013), ETSP (Galán et al., 2009; Kalvelage et al., 2013), Colombian Pacific (Castro-González et al., 2014), Arabian Sea (Jaeschke et al., 2007; Lam et al., 2011), Eastern Indian Ocean (Qian et al., 2018) and Namibian upwelling system (Woebken et al., 2007; Kalvelage et al., 2011), where the anammox process accounts for between one-fifth and all of N_2 production (Dalsgaard et al., 2005). In fact, anammox may be the dominant N-loss pathway in the OMZs of Namibia (Kuypers et al., 2005) and ETSP (Hamersley et al., 2007); although higher denitrification rates have also been found in the ETSP, suggesting that both processes may be temporally and/or spatially separated (Dalsgaard et al., 2012).

A low diversity of anammox communities has been detected in OMZs (Schmid et al., 2007; Kong et al., 2013), in which two clades of *Ca*. Scalindua typically predominate: Clade 1 (*Ca.* Scalindua sorokinii/brodae) and clade 2 (*Ca*. Scalindua arabica) (Woebken et al., 2008). *Ca.* Scalindua species also split into two clusters in the Black Sea: *Ca.* Scalindua richardsii, present in the upper suboxic zone at high NO_2^- and NO_3^- and low NH_4^+ concentrations, and *Ca.* Scalindua sorokinii, present in the

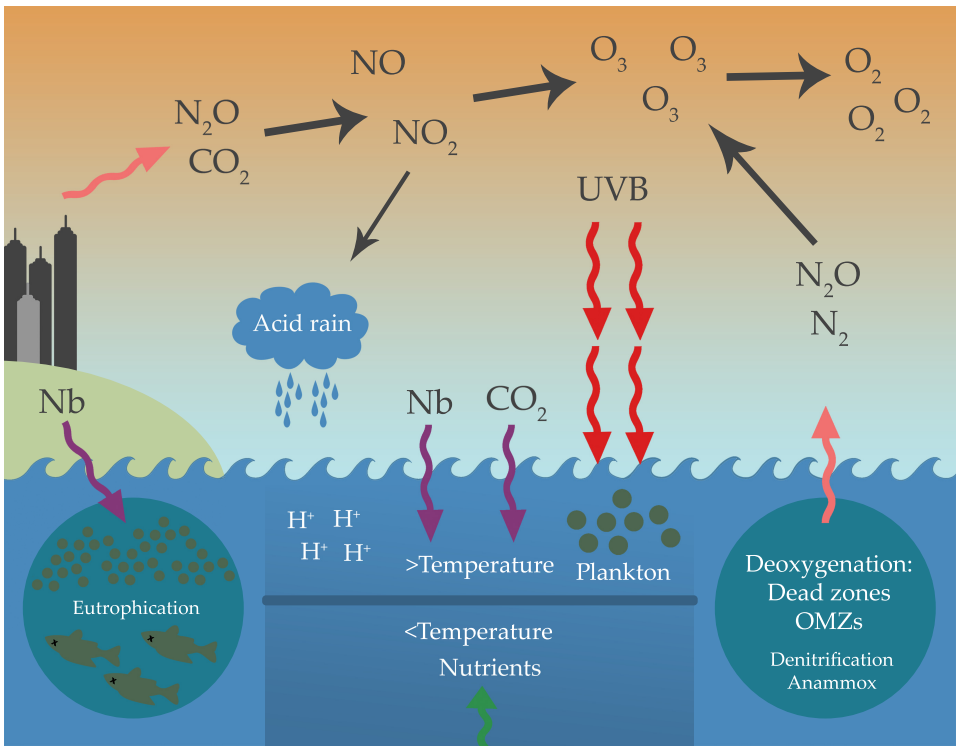

FIGURE 3 | Anthropogenic activities and their effects on the marine N cycling. Bioavailable N (Nb) is introduced into the marine ecosystems by runoff or atmospheric deposition, causing eutrophication, the formation of dead zones and the expansion of the ocean minimum zones (OMZs). The release of N oxides (N_2O, NO) from anthropogenic activities and oxygen-depleted zones causes stratospheric ozone depletion leading to higher UVB exposition, which produces the damage of marine life, acid rain and ocean warming. Ocean warming causes water stratification, deoxygenation, and the formation of dead zones. Dead zones and OMZs are hotspots for anammox and denitrification, causing N loss (N_2 and N_2O). Elevated atmospheric CO_2 acidifies seawater, decreasing pH-dependent N-cycling processes such as nitrification, and enhancing N_2 fixation.

lower suboxic zone at high NH_4^+ and low NO_3^- concentrations (Fuchsman et al., 2012).

Estuaries and coastal environments. Anammox has been reported mainly in eutrophic estuaries (e.g., Trimmer et al., 2003; Risgaard-Petersen et al., 2004; Lisa et al., 2015) and coastal sediments (e.g., Engström et al., 2005; Tal et al., 2005; Dang et al., 2013), where the distribution of anammox bacterial diversity and activity is mostly affected by temperature, salinity, NO_3^- and organic N substrates (Hou et al., 2013; Brin et al., 2014; Sonthiphand et al., 2014). *Ca.* Scalindua typically dominates throughout estuarine sediments (Tal et al., 2005; Rich et al., 2008; Dang et al., 2010a) while *Ca.* Brocadia, *Ca.* Kuenenia, *Ca.* Anammoxoglobous and *Ca.* Jettenia are mainly found in fresh to oligohaline sediments (Dale et al., 2009; Hirsch et al., 2011).

Deep-sea and other environments. Deep-sea and other extreme environments harbor a great diversity and abundance of *Ca.* Scalindua species (Hong et al., 2011a,b; Shehzad et al., 2016). Anammox bacteria are also active in hydrothermal vent areas such as those in the Mid-Atlantic Ridge, where anammox occurs as high as 85°C (Byrne et al., 2009), the Okhotsk Sea, where *hzo* is highly abundant (Shao et al., 2014), and the Guaymas Basin, where *Ca.* Scalindua species are more abundant in cold hydrocarbon-rich sediments than hydrothermal vents (Russ et al., 2013).

EFFECTS OF ANTHROPOGENIC ACTIVITY ON THE MARINE NITROGEN CYCLE

The marine N cycle is being largely perturbed by human activity. Anthropogenic activities pertaining to the production of artificial fertilizers and fossil fuel combustion are mainly responsible for this imbalance, affecting the marine N cycle directly or indirectly (**Figure 3**). Direct alterations include the N inputs through riverine discharges and atmospheric deposition (Duce et al., 2008; Lee et al., 2016; Jickells et al., 2017) that cause eutrophication and the formation of anoxic or hypoxic areas in coastal areas ("dead zones"), impacting primary production and the marine trophic web (Vaquer-Sunyer and Duarte, 2008). Indirect alterations include activities that increase the atmospheric concentration of greenhouse gases, leading to ocean warming, acidification and deoxygenation. The impacts of these alterations on the marine N cycle remain highly uncertain (Gruber, 2016; Hutchins and Fu, 2017) and have been covered by multiple reviews (e.g., Voss et al., 2013; Wannicke et al., 2018).

BOX 1 | Priority research topics on the marine N cycle.

- Further studying of the physiology, metabolism, genetics, and ecology of microorganisms participating in novel and previously established N-cycling processes (e.g., UCYN groups, heterotrophic diazotrophs, AOA clades, NOB, DNRA communities, ANME-2d, NC10 bacteria, anammox bacteria).
- Exploring N processes in understudied marine systems (e.g., BNF in coastal zones, nitrification and denitrification in coral reefs, comammox in the ocean, anaerobic N processes in sinking particles, and N processes in deep sea environments).
- Investigating the interactions and couplings between N cycle processes.
- A more comprehensive understanding of the environmental and ecological interaction between N-gain and N-loss processes in order to advance toward a more robust estimates and predictions of the marine N budget.
- A mechanistic understanding of the potential effects of anthropogenic activity on marine N processes and their interaction with other biogeochemical processes.

Many studies have been conducted on the response of BNF in the future ocean. Recent models indicate that increased atmospheric N deposition will slow down BNF rates due to the enhanced availability of fixed N in the surface ocean (Somes et al., 2016; Yang and Gruber, 2016; Jickells et al., 2017). However, these models do not take in consideration other future ocean scenarios such as ocean acidification or warming. Several studies show that ocean acidification does not seem to have an effect on C and N_2 fixation rates in mixed diazotrophic assemblages (Law et al., 2012; Böttjer et al., 2014). Conversely, other studies have documented the increase of C and N_2 fixation rates in *Trichodesmium* and UCYN-B cultures when CO_2 levels are increased to those expected in the future ocean (e.g., Lomas et al., 2012; Hutchins et al., 2015; Rees et al., 2017). This species-specific response of N_2 fixation to ocean acidification may impact on the dominance of diazotrophic groups and also alter new N supply to the ocean; although this response seems to be dependent on light, P, and Fe (Hutchins et al., 2013). More studies on this topic are needed, since ocean acidification may lead to a decrease in the bioavailability of Fe (Shi et al., 2010), which may in turn lead to a decrease in BNF. Furthermore, ocean warming will likely cause an expansion of habitats suitable for diazotrophs and an increase of BNF (Hutchins et al., 2009; Sohm et al., 2011b), leading to an increase of available N for further processes in the N cycle.

Nitrification rates may decrease as a consequence of ocean acidification. Experiments have demonstrated decreases in NH_3 oxidation due to the incremental protonation of NH_3 to NH_4^+ as seawater pH decreases (Beman et al., 2011; Kitidis et al., 2011). A decrease in nitrification rates may reduce the supply of NO_2^- and NO_3^- to other N-cycling processes such as denitrification, anammox and DNRA, turning nitrification into a "N cycle bottleneck" (Hutchins et al., 2009) and putting NO_3^--consumers in disadvantage over NH_4^+-consumers (Yool et al., 2007). Furthermore, a decrease in nitrification rates due to ocean acidification could reduce N_2O production between 2.4 and 44% (Beman et al., 2011; Rees et al., 2016). In contrast, nitrification rates might exhibit an increase due to a "CO_2-fertilization" effect (Hutchins et al., 2009); however, this assumption need to be further demonstrated, as evidence suggest that this is unlikely to happen given that AOA lack RuBisCo (Walker et al., 2010) and AOB possess mechanisms to reduce their sensibility to CO_2 (Chain et al., 2003).

Little is known about how ocean warming may affect nitrification, but studies suggest that ammonia oxidizers may be relatively insensitive to changing temperature (Horak et al., 2013; Baer et al., 2014). Conversely, the global proliferation of suboxic waters as consequence of deoxygenation could promote nitrification, since this process occurs in transitional regions around OMZs where O_2 is low but not fully depleted (Newell et al., 2011; Peng et al., 2015; Bristow et al., 2016).

Ammonia oxidation and denitrification are the major sources of marine N_2O, but their contribution to the global N_2O budget and the factors controlling its production and consumption are still being investigated. Moreover, the consequences of anthropogenic activities on N-loss processes have not been properly investigated. No direct effect of ocean acidification has been observed on these processes (Wannicke et al., 2018); although an increase in marine pCO_2 may result in an elevated C:N ratio, indirectly enhancing denitrification (Hutchins et al., 2009) and decreasing anammox (Babbin et al., 2014). Models have also suggested that increased atmospheric N deposition and deoxygenation could enhance denitrification (Keeling et al., 2010; Somes et al., 2016; Yang and Gruber, 2016; Jickells et al., 2017), which in turn may increase by 21% the marine N_2O production (Battaglia and Joos, 2018).

Alterations in the N cycling will also have mayor consequences for marine C cycling. However, the understanding of these consequences is poor due to the lack of enough global models. Some of these collateral alterations include modifications to CO_2 budgets as result of elevated primary production due to the increase of available N entering marine ecosystems. Calculations suggest that atmospheric N deposition represents ∼32% of the total N entering the ocean, which translates into ∼3% of the annual new marine production (∼0.3 Pg C yr^{-1}) (Duce et al., 2008). Other authors have estimated that anthropogenic atmospheric N inputs are currently leading to an increase in primary production and CO_2 uptake of 0.15 Pg C yr^{-1} (Jickells et al., 2017). However, the resulting reduction in radiative forcing will be offset by increases in marine N_2O emissions (Suntharalingam et al., 2012). Further, the CO_2 budgets could also be altered as result of an increase of hypoxia and denitrification generated by N inputs in coastal environments. In addition, the dominance of either denitrification or anammox in expanding dead zones and OMZs will impact global C and N budgets. In marine environments dominated by denitrification, CO_2 and N_2O emissions are likely to increase, while in environments dominated by anammox, atmospheric CO_2 uptake is likely to increase (Koeve and Kähler, 2010; Suntharalingam et al., 2012).

CONCLUSION AND PERSPECTIVES

In this review, we have provided a panorama of the genetics, ecology and distribution of marine N-cycling microbes and the processes they mediate. These processes are more widely distributed than previously thought, given that they have been found in unpredicted marine environments. Plus, many new metabolic N pathways have been reported over the past few years, completely changing the paradigm of the classic marine N cycle. Additionally, we have examined the potential effects of human activity on N processes; such activity has led to an alteration of the natural balance of the marine N cycle, with consequences that we are just beginning to experience and comprehend. Many models have been developed to help us foresee the consequences of anthropogenic activities on the marine N cycle. However, these mathematical representations of the future cannot be completely trusted as they have been developed based on our current understating of the N processes, and we still have a long way to go given that new discoveries are made every day. Thus, we need to build models based on an holistic view of the processes and scenarios, using all the available information and taking into consideration all the possible natural settings. To do this, we should first understand the functioning of the microorganisms involved in the marine N processes. Finally, we identify potential priority research topics regarding marine microbial N cycle in which future investigation should be directed (**Box 1**).

AUTHOR CONTRIBUTIONS

All authors listed have made a substantial, direct and intellectual contribution to the work, and approved it for publication.

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