



1 Database of nitrification and nitrifiers in the global ocean

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34



35 Abstract

36 As a key biogeochemical pathway in the marine nitrogen cycle, nitrification (ammonia oxidation
37 and nitrite oxidation) converts the most reduced form of nitrogen – ammonium/ammonia (NH_4^+ /
38 NH_3) into the oxidized species nitrite (NO_2^-) and nitrate (NO_3^-). In the ocean, these processes are
39 mainly performed by ammonia-oxidizing archaea (AOA) and bacteria (AOB), and nitrite-
40 oxidizing bacteria (NOB). By transforming nitrogen speciation and providing substrates for
41 nitrogen removal, nitrification affects microbial community structure, marine productivity
42 (including chemoautotrophic carbon fixation) and the production of a powerful greenhouse gas,
43 nitrous oxide (N_2O). Nitrification is hypothesized to be regulated by temperature, oxygen, light,
44 substrate concentration, substrate flux, pH, and other environmental factors. Although the number
45 of field observations from various oceanic regions has increased considerably over the last few
46 decades, a global synthesis is lacking, and understanding how environmental factors control
47 nitrification remains elusive. Therefore, we have compiled a database of nitrification rates and
48 nitrifier abundance in the global ocean from published literature and unpublished datasets. This
49 database includes 2393 and 1006 measurements of ammonia oxidation and nitrite oxidation rates,
50 and 2187 and 631 quantifications of ammonia oxidizers and nitrite oxidizers, respectively. This
51 community effort confirms and enhances our understanding of the spatial distribution of
52 nitrification and nitrifiers, and their corresponding drivers such as the important role of substrate
53 concentration in controlling nitrification rates and nitrifier abundance. Some conundrums are also
54 revealed including the inconsistent observations of light limitation and high rates of nitrite
55 oxidation reported from anoxic waters. This database can be used to constrain the distribution of
56 marine nitrification, to evaluate and improve biogeochemical models of nitrification, and to
57 quantify the impact of nitrification on ecosystem functions like marine productivity and N_2O
58 production. This database additionally sets a baseline for comparison with future observations and
59 guides future exploration (e.g., measurements in the poorly sampled regions such as the Indian
60 Ocean; method comparison/standardization). The database is publicly available at Zenodo
61 repository: <https://doi.org/10.5281/zenodo.7942922> (Tang et al., 2023).

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63 Introduction

64 Nitrification (ammonia oxidation and nitrite oxidation) converts the most reduced form of nitrogen
65 (N) – ammonium/ammonia ($\text{NH}_4^+/\text{NH}_3$) into the oxidized compounds nitrite (NO_2^-) and nitrate
66 (NO_3^-). Ammonia oxidation is conducted by ammonia oxidizing archaea (AOA) and bacteria
67 (AOB) with AOA dominating in most marine environments (Francis et al., 2005; Wuchter et al.,
68 2006). Marine AOA are often separated into a few major ecotype groups including water column
69 group A, water column group B and *Nitrosopumilus*-like (Beman et al., 2008; Tolar et al., 2020),
70 with a diverse group of AOA remaining to be characterized (Alves et al., 2018). Marine nitrite
71 oxidation is carried out by nitrite-oxidizing bacteria (NOB) such as *Nitrospina*, *Nitrospira*,
72 *Nitrococcus* and *Nitrobacter*, with *Nitrospina* as the dominant group (Mincer et al., 2007;
73 Pachiadaki et al., 2017). Complete ammonia-oxidizing (comammox) bacteria within the bacterial
74 genus *Nitrospira* have been identified in freshwater, terrestrial, and coastal environments but not
75 yet been found in the open ocean (Daims et al., 2015; Van Kessel et al., 2015; Xia et al., 2018).

76

77 Nitrification and nitrifiers are thought to be regulated by light/solar radiation, oxygen, temperature,
78 substrate concentration, pH, and other environmental factors (Ward, 2008), many of which are
79 experiencing dramatic changes in the ocean. For example, light is generally found to inhibit
80 nitrifiers' growth and nitrification rate (Olson, 1981b; Merbt et al., 2012; Xu et al., 2019). In
81 addition, ocean acidification decreases ammonia oxidation rates (Beman et al., 2011; Breider et
82 al., 2019) partly due to the decreased availability at lower pH of NH_3 , which is the actual substrate
83 for ammonia oxidation (Suzuki et al., 1974). In contrast, ocean warming shifts the $\text{NH}_4^+/\text{NH}_3$
84 equilibrium towards NH_3 by decreasing the pK_a (Emerson et al., 1975) and is observed to enhance
85 enzyme activity (Zheng et al., 2017; Zheng et al., 2020), further complicating the effect of climate
86 change on nitrification.

87

88 Although nitrification does not directly change the absolute inventory of bioavailable N, it can
89 control the relative availability of substrates (NH_4^+ , NO_2^- and NO_3^-) for phytoplankton growth.
90 Since prokaryotic phytoplankton preferentially assimilate NH_4^+ while eukaryotic phytoplankton
91 are better able to exploit NO_3^- in the sunlit surface ocean (Berthelot et al., 2018; Fawcett et al.,
92 2011), variations in the relative supply of NH_4^+ versus NO_3^- can influence phytoplankton
93 community composition and ecosystem functionalities. Because the uptakes of NH_4^+ and NO_3^- are



94 often used to differentiate regenerated and new production (Eppley and Peterson, 1979),
95 production of NO_3^- by nitrification in the surface ocean may bias the estimate of new production
96 (Yool et al., 2007). NO_2^- and NO_3^- are also involved in denitrification and anammox, which remove
97 bioavailable N from the ocean. Thus, nitrification can indirectly affect the size of the bioavailable
98 N pool, marine productivity and ultimately the atmospheric CO_2 concentration (Falkowski, 1997).
99 As a chemoautotrophic process, nitrification in the ocean water column is estimated to supply
100 $\sim 0.13\text{-}1.4 \text{ Pg C yr}^{-1}$ of organic matter, which is critical to support the heterotrophic microbial
101 community/metabolism in the dark ocean (Bayer et al., 2022; Middelburg, 2011; Pachiadaki et al.,
102 2017; Zhang et al., 2020). Nitrification could also contribute to the oxygen consumption and the
103 development of hypoxia or anoxia (Hsiao et al., 2014; Beman et al., 2021). In addition, nitrification
104 is the major global ocean source of N_2O , a potent greenhouse gas and dominant ozone-depleting
105 agent, thus connecting the marine N cycle directly to the Earth's climate system (Freing et al.,
106 2012; Ji et al., 2018).

107

108 Considering the important role of nitrification and nitrifiers in marine N and C cycles and Earth's
109 climate, a better understanding of its distribution and regulating factors is highly desirable.
110 Historical observations of nitrification and nitrifiers cover a wide range of environmental gradients
111 and biogeography in the ocean, ranging from cross-Atlantic (e.g., Clark et al., 2008; Clark et al.,
112 2022), western Pacific (e.g., Wan et al., 2021; Wan et al., 2018), polar oceans (e.g., Shiozaki et
113 al., 2019; Mduyana et al., 2020) to oxygen minimum zones (e.g., Peng et al., 2015; Santoro et al.,
114 2021). This study aims to introduce the newly constructed database of nitrification and nitrifiers
115 in the marine water column and to guide future research efforts in field observations and model
116 development of nitrification. This new global synthesis significantly expands upon what was
117 possible with earlier more limited datasets (Yool et al. 2007; Ward, 2008). Additional reviews on
118 marine nitrification and nitrifiers can be found elsewhere (Schleper and Nicol, 2010; Daims et al.,
119 2016; Ward, 2011b).

120



121 **Methods**

122 **Data sources and compilation**

123 Nitrification rates including ammonia oxidation and nitrite oxidation, and abundances of ammonia
 124 oxidizers and nitrite oxidizers were extracted directly from the literature published between 1984
 125 and 2022 when the data were presented in tables or supplementary materials from publications;
 126 otherwise, data were provided by the coauthors. Some previously unpublished data were also
 127 included in the database. Table 1 and Table 2 summarize the origin, methods and locations of
 128 nitrification rate and nitrifier abundance measurements, sorted in alphabetical order by lead author.
 129 The metadata format contains geographical sampling information (date, latitude, longitude, and
 130 depth) and concurrent measurements of environmental conditions such as light intensity,
 131 temperature, salinity, water density, N concentration (NH_4^+ , NO_2^- and NO_3^-), pH and oxygen
 132 concentration if available. In total, there are 2393, 1006, 2187, and 631 measurements of ammonia
 133 oxidation rate, nitrite oxidation rate, ammonia oxidizer abundance and nitrite oxidizer abundance,
 134 respectively. However, not all measurements of nitrification rates or nitrifier abundance are
 135 accompanied by all the environmental factors because such factors were often not reported in the
 136 literature or recorded during the measurements/sample collections. Rates, nitrifier abundances and
 137 environmental parameters below the methodological detection limits are noted as BDL. NM
 138 represents parameters that were not measured. Empty/NA means that data are not available or
 139 reported. The database is deposited into Zenodo repository following the Findable, Accessible,
 140 Interoperable and Reusable (FAIR) principles for data management (Wilkinson et al., 2016). We
 141 encourage authors and readers to contact us to report an update to or an error in the database.

142

143 Table 1. Summary of the number of observations for nitrification rates in alphabetical order of the
 144 lead author. The method (e.g., substrate tracer addition vs product dilution) and sampling regions
 145 are listed. Methods used for data collection are described in the next section.

References	Ammonia oxidation	Nitrification				Sampling regions
		Method	Analyte	Nitrite oxidation	Method	
Baer et al., 2017	6	$^{15}\text{NH}_4^+$ tracer addition	NO_2^- NO_3^-			Western Coastal Arctic



Beman et al., 2012	68	$^{15}\text{NH}_4^+$ addition	tracer	$\text{NO}_2^- + \text{NO}_3^-$	64	$^{15}\text{NO}_2^-$ addition	tracer	Eastern Tropical North Pacific
Beman et al., 2021	78	$^{15}\text{NH}_4^+$ addition	tracer	$\text{NO}_2^- + \text{NO}_3^-$	79	$^{15}\text{NO}_2^-$ addition	tracer	Eastern Tropical North Pacific
Bianchi et al., 1997	21	$\text{H}^{14}\text{CO}_3^-$ addition	tracer	Particulate organic carbon	21	$\text{H}^{14}\text{CO}_3^-$ addition	tracer	Southern Ocean
Breider et al., 2019	10	$^{15}\text{NH}_4^+$ addition	tracer	$\text{NO}_2^- + \text{NO}_3^-$				Western North Pacific
Bristow et al., 2015	9	$^{15}\text{NH}_4^+$ addition	tracer	NO_2^-	9	$^{15}\text{NO}_2^-$ addition	tracer	Gulf of Mexico
Cavagna et al., 2015					39	$^{15}\text{NO}_3^-$ dilution	tracer	Southern Ocean
Clark et al., 2008	32	$^{15}\text{NO}_2^-$ dilution	tracer	NO_2^-	32	$^{15}\text{NO}_3^-$ dilution	tracer	Atlantic
Clark et al., 2011	13	$^{15}\text{NO}_2^-$ dilution	tracer	NO_2^-	13	$^{15}\text{NO}_3^-$ dilution	tracer	Eastern North Atlantic (offshore of the Iberian Peninsula)
Clark et al., 2014	10	$^{15}\text{NO}_2^-$ dilution	tracer	NO_2^-	10	$^{15}\text{NO}_3^-$ dilution	tracer	Northwest European shelf sea
Clark et al., 2016	21	$^{15}\text{NO}_2^-$ dilution	tracer	NO_2^-	42	$^{15}\text{NO}_3^-$ dilution	tracer	Mauritanian upwelling system
Clark et al., 2022	88	$^{15}\text{NO}_2^-$ dilution	tracer	NO_2^-				Atlantic
Clark et al., unpublished 1	18	$^{15}\text{NO}_2^-$ dilution	tracer	NO_2^-	18	$^{15}\text{NO}_3^-$ dilution	tracer	Eastern North Atlantic
Clark et al., unpublished 2	18	$^{15}\text{NO}_2^-$ dilution	tracer	NO_2^-	18	$^{15}\text{NO}_3^-$ dilution	tracer	Eastern North Atlantic
Clark et al., unpublished 3	21	$^{15}\text{NO}_2^-$ dilution	tracer	NO_2^-	21	$^{15}\text{NO}_3^-$ dilution	tracer	Eastern North Atlantic
Clark et al., unpublished 4	11	$^{15}\text{NO}_2^-$ dilution	tracer	NO_2^-	11	$^{15}\text{NO}_3^-$ dilution	tracer	Subpolar North Atlantic and Arctic



Damashek et al., 2018	15	$^{15}\text{NH}_4^+$ tracer addition	NO_2^- NO_3^-				South Atlantic Bight
Diaz and Raimbault, 2000	20	$^{15}\text{NH}_4^+$ tracer addition	NO_2^- NO_3^-				Gulf of Lions in the Mediterranean Sea
Dore and Karl, 1996	11	NO_2^- concentration change over time; $\text{H}^{14}\text{CO}_3^-$ tracer addition	NO_2^- NO_3^- , particulate organic carbon	6	NO_3^- concentration change over time		Station ALOHA in the North Pacific
Fernández et al., 2009	15	$^{15}\text{NH}_4^+$ tracer addition	NO_2^- NO_3^-				Peru upwelling system
Flynn et al., 2021				104	$^{15}\text{NO}_2^-$ tracer addition		Weddell Sea
Frey et al., 2020	21	$^{15}\text{NH}_4^+$ tracer addition	NO_2^-				Eastern Tropical South Pacific
Frey et al., 2022	30	$^{15}\text{NH}_4^+$ tracer addition	NO_2^-				Eastern Tropical North Pacific
Ganesh et al., 2015	5	$^{15}\text{NH}_4^+$ tracer addition	NO_2^-	5	$^{15}\text{NO}_2^-$ tracer addition		Eastern Tropical North Pacific oxygen minimum zone
Kalvelage et al., 2011	6	$^{15}\text{NH}_4^+$ tracer addition	NO_2^-				Namibian oxygen minimum zone
Kalvelage et al., 2013	108	$^{15}\text{NH}_4^+$ tracer addition	NO_2^-	110	$^{15}\text{NO}_2^-$ tracer addition		Eastern Tropical South Pacific oxygen minimum zone
Kitzinger et al., 2020	9	$^{15}\text{NH}_4^+$ tracer addition	NO_2^-	9	$^{15}\text{NO}_2^-$ tracer addition		Gulf of Mexico
Lam et al., 2009	14	$^{15}\text{NH}_4^+$ tracer addition	NO_2^-				Eastern Tropical South Pacific
Laperriere et al., 2020	59	$^{15}\text{NH}_4^+$ tracer addition	NO_2^- NO_3^-				Southern California Bight



Liu et al., 2018	86	$^{15}\text{NH}_4^+$ addition	tracer	NO_2^-+ NO_3^-			South Atlantic Bight
Liu et al., 2022	10	$^{15}\text{NH}_4^+$ addition	tracer	NO_2^-+ NO_3^-			South China Sea
Mccarthy et al., 1999	8	$^{15}\text{NH}_4^+$ addition	tracer	NO_2^-+ NO_3^-			Arabian Sea
Mdutyana et al., 2020	59	$^{15}\text{NH}_4^+$ addition	tracer	NO_2^-	38	$^{15}\text{NO}_2^-$ tracer addition	Southern Ocean
Mdutyana et al., 2022a	24	$^{15}\text{NH}_4^+$ addition	tracer	NO_2^-			Southern Ocean
Mdutyana et al., 2022b					24	$^{15}\text{NO}_2^-$ tracer addition	Southern Ocean
Newell et al., 2013	8	$^{15}\text{NH}_4^+$ addition	tracer	NO_2^-			Sargasso Sea (western North Pacific)
Peng et al., 2015	30	$^{15}\text{NH}_4^+$ addition	tracer	NO_2^- , NO_2^-+ NO_3^-	30	$^{15}\text{NO}_2^-$ tracer addition	Eastern Tropical North Pacific
Peng et al., 2016	47	$^{15}\text{NH}_4^+$ addition	tracer	NO_2^-	47	$^{15}\text{NO}_2^-$ tracer addition	Eastern Tropical South Pacific
Peng et al., 2018	28	$^{15}\text{NH}_4^+$ addition	tracer	NO_2^-	28	$^{15}\text{NO}_2^-$ tracer addition	Subarctic North Atlantic
Raes et al., 2020	39	$^{15}\text{NH}_4^+$ addition	tracer	NO_2^-+ NO_3^-			South Pacific
Raimbault et al., 1999	41	$^{15}\text{NH}_4^+$ addition	tracer	NO_2^-+ NO_3^-			Equatorial Pacific
Santoro et al., 2010	11	$^{15}\text{NH}_4^+$ addition	tracer	NO_2^-+ NO_3^-			Central California Current
Santoro et al., 2013	10	$^{15}\text{NH}_4^+$ addition	tracer	NO_2^- , NO_2^-+ NO_3^-			Central California Current
Santoro et al., 2017	12	$^{15}\text{NH}_4^+$ addition	tracer	NO_2^-+ NO_3^-			Equatorial Pacific
Santoro et al., 2021	57	$^{15}\text{NH}_4^+$ addition	tracer	NO_2^-+ NO_3^-	57	$^{15}\text{NO}_2^-$ tracer addition	Eastern Tropical South Pacific



Sinyanya et al., unpublished				31	$^{15}\text{NO}_2^-$ tracer addition	Southwest Indian Ocean
Shiozaki et al., 2016	87	$^{15}\text{NH}_4^+$ tracer addition	$\text{NO}_2^- + \text{NO}_3^-$			Equatorial Pacific to the Arctic Ocean
Shiozaki et al., 2019	56	$^{15}\text{NH}_4^+$ tracer addition	$\text{NO}_2^- + \text{NO}_3^-$			Arctic Ocean
Shiozaki et al., 2021	28	$^{15}\text{NH}_4^+$ tracer addition	$\text{NO}_2^- + \text{NO}_3^-$			Arctic Ocean
Smith et al., 2022	11	$^{15}\text{NH}_4^+$ tracer addition	NO_2^-			Southern Ocean
Sun et al., 2017				9	$^{15}\text{NO}_2^-$ tracer addition	Eastern Tropical North Pacific
Sutka et al., 2004	20	$^{15}\text{NH}_4^+$ tracer addition	$\text{NO}_2^- + \text{NO}_3^-$			North Pacific Subtropical Gyre to Eastern Tropical North Pacific
Tolar et al., 2016	73	$^{15}\text{NH}_4^+$ tracer addition	$\text{NO}_2^- + \text{NO}_3^-$			Antarctic coast
Tolar et al., 2017	38	$^{15}\text{NH}_4^+$ tracer addition	$\text{NO}_2^- + \text{NO}_3^-$			Georgia coast, South Atlantic Bight, Gulf of Alaska, Antarctic coast
Tolar et al., 2020	297	$^{15}\text{NH}_4^+$ tracer addition	$\text{NO}_2^- + \text{NO}_3^-$			Monterey Bay
Wallschuss et al., 2022	40	$^{15}\text{NH}_4^+$ tracer addition	NO_2^-	40	$^{15}\text{NO}_2^-$ tracer addition	Southeastern Atlantic
Wan et al., 2018	90	$^{15}\text{NH}_4^+$ tracer addition	$\text{NO}_2^- + \text{NO}_3^-$			South China Sea and Northwest Pacific
Wan et al., 2021	17	$^{15}\text{NH}_4^+$ tracer addition	NO_2^-	17	$^{15}\text{NO}_2^-$ tracer addition	North Pacific
Wan et al., 2022	85	$^{15}\text{NH}_4^+$ tracer addition	NO_2^-			North Pacific



Ward et al., 1984	16	$^{15}\text{NH}_4^+$ addition	tracer	NO_2^-			Coastal waters off Washington
Ward, 1987	24	$^{15}\text{NH}_4^+$ addition	tracer	NO_2^-		$^{15}\text{NO}_2^-$ addition	Southern California Bight
Ward and Zafriou, 1988	42	$^{15}\text{NH}_4^+$ addition	tracer	NO_2^-			Eastern Tropical North Pacific
Ward et al., 1989	47	$^{15}\text{NH}_4^+$ addition	tracer	NO_2^-	47	$^{15}\text{NO}_2^-$ addition	Eastern Tropical South Pacific
Ward, 2005	110	$^{15}\text{NH}_4^+$ addition	tracer	NO_2^-			Monterey Bay
Xu et al., 2018	78	$^{15}\text{NH}_4^+$ addition	tracer	NO_2^-			South China Sea
Zhang et al., 2020	27	$^{15}\text{NH}_4^+$ addition	tracer	NO_2^-	27	$^{15}\text{NO}_2^-$ addition	South China Sea and Western Pacific
Total number of observations	2393				1006		

146

147 Table 2. Summary of the number of observations for nitrifier abundance from qPCR assays in
 148 alphabetical order of the lead authors. The top row indicates the gene quantified for each group
 149 (see text for further details). The primers used for individual studies are identified in the database.
 150 AOA: ammonia-oxidizing archaea; AOB: ammonia-oxidizing bacteria; NOB: nitrite-oxidizing
 151 bacteria.

References	<i>amoA</i> -based		<i>nxr</i> -based	<i>16S rRNA</i> -based			Sampling regions
	AOA	AOB	NOB	<i>Thaumarchaeota</i>	<i>Nitrospira</i>	<i>Nitrospina</i>	
Agogue et al., 2008	55	55		55			North Atlantic
Beman et al., 2012	64	64		64			Eastern Tropical North Pacific
Beman et al., 2013						63	Eastern Tropical North Pacific
Bristow et al., 2016b	27		27				Bay of Bengal oxygen minimum zone



Damashek et al., 2018.	34			34		34	South Atlantic Bight
Frey et al., 2020	21						South Pacific oxygen minimum zone
Frey et al., 2022	30						North Pacific oxygen minimum zone
Horak et al., 2018	6	6					North Pacific Ocean
Kalvelage et al., 2013.	143	89					South Pacific oxygen minimum zone
Liu et al., 2018.	385	385		385		385	South Atlantic Bight
Peng et al., 2013	23						Eastern Tropical North Pacific
Peng et a., 2015	19	19					Eastern Tropical South Pacific
Peng et a., 2016	19	19					Subarctic North Atlantic
Santoro et al., 2010	17	17		17		17	Central California Current
Santoro et al., 2013	10	10					Central California Current
Santoro et al., 2017	148						Equatorial Pacific
Santoro et al., 2021	78	24		78		78	Eastern Tropical South Pacific
Shiozaki et al., 2016	87	87					North Pacific
Shiozaki et al., 2019	56	56					Arctic Ocean
Shiozaki et al., 2021	28	28					Arctic Ocean
Sintes et al., 2013	115			115			Tropical Atlantic and coastal Arctic



Sintes et al., 2016	364			364			Atlantic Ocean
Tolar et al., 2016	73	73					Antarctic coast
Tolar et al., 2017	38			38			Georgia coast, South Atlantic Bight, Gulf of Alaska, Antarctic coast
Tolar et al., 2020	297						Monterey Bay
Wuchter et al., 2006	20	20		20			Atlantic Ocean
Zakem et al., 2018	31						North Pacific
Zhang et al., 2020	54	54		54	54	54	South China Sea and Western Pacific
Total points	2187	951	27	1169	54	631	

152

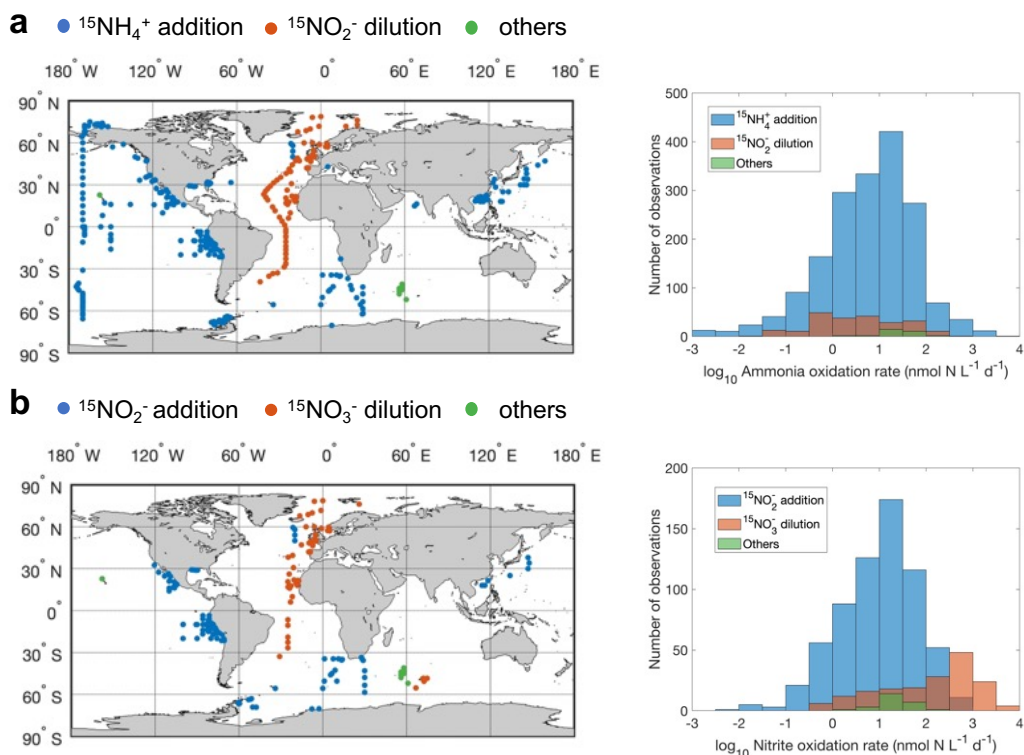
153 We applied Chauvenet's criterion for quality control to flag outliers in nitrification rates and
 154 nitrifier abundance (Glover et al., 2011). Chauvenet's criterion is commonly applied to normally
 155 distributed datasets to identify outliers whose deviations from the mean have a probability of less
 156 than $1/(2n)$, where n is the number of data points (Buitenhuis et al., 2013). We applied the criterion
 157 acknowledging the fact that the data were collected at different environmental conditions. After
 158 removing measurements of zero and below detection limit, nitrification rates and nitrifier
 159 abundances were log₁₀ transformed before further analysis. Nitrification rates and nitrifier
 160 abundances reported at 0 or below detection limit are noted separately in the database and
 161 following analysis. Although we did not find outliers for ammonia oxidation and nitrite oxidation
 162 rates, there are some extreme values worth noting. For example, an extremely high ammonia
 163 oxidation rate of 4900 nmol L⁻¹ d⁻¹ was observed in the Peruvian oxygen minimum zone (Lam et
 164 al., 2009). Low but detectable rates below 0.01 nmol L⁻¹ d⁻¹ were observed in the Eastern Tropical
 165 North Pacific oxygen minimum zone (Frey et al., 2022), South Atlantic Bight (Liu et al., 2018)
 166 and western Pacific (Xu et al., 2018). Some outliers were identified by Chauvenet's criterion for
 167 ammonia oxidizers. For instance, an abnormally high abundance of the bacterial *amoA* gene (10⁸
 168 copies L⁻¹) was observed in the South Pacific oxygen minimum zone (Kalvelage et al., 2013),
 169 which was removed from the following analysis. A low abundance of 16S rRNA of
 170 *Thaumarchaeota* (25 copies L⁻¹) was found in the surface water of the western Pacific (Zhang et



171 al., 2020). In addition, the low-ammonia concentration AOA ecotype (or water column group B
172 AOA) at 2 copies L⁻¹ was reported in the Arctic Ocean (Sintes et al., 2013). Measurements of
173 nitrification rate and nitrifier abundance of 0 or below detection limit were not included in the
174 analysis of outlier identification. For example, AOA abundance at 0 or below detection limit
175 (varies among studies) has been reported in surface waters of South Atlantic Bight (Damashek et
176 al., 2018), equatorial Pacific (Santoro et al., 2017) and North Pacific (Shiozaki et al., 2016).
177

178 **Methods for measuring ammonia oxidation and nitrite oxidation rates**

179 Ammonia oxidation rate is commonly measured by comparing the change in nitrite (NO₂⁻) and
180 nitrate (NO₃⁻) concentration in controls versus an experimental treatment containing a nitrification
181 inhibitor (e.g., Dore and Karl, 1996), by tracking the oxidation of ¹⁵NH₄⁺ into the NO₂⁻ and NO₃⁻
182 pool (Olson, 1981a), or by the dilution of ¹⁵NO₂⁻ (Clark et al., 2007). Similarly, nitrite oxidation
183 rate can be measured by the change in NO₃⁻ concentration, by tracking the oxidation of ¹⁵NO₂⁻ into
184 the NO₃⁻ pool, or by the dilution of ¹⁵NO₃⁻ (Ward et al., 1989). In addition, nitrification has also
185 been estimated from the incorporation of ¹⁴C tracer due to the chemoautotrophic metabolism of
186 nitrifiers (Bianchi et al., 1997). There is a large uncertainty, however, in the conversion factor from
187 carbon fixation to nitrification (Bayer et al., 2022). A more detailed description of methods for
188 measuring nitrification can be found in Ward, 2011a. The spatial distribution of different methods
189 used to measure nitrification and the frequency distribution of measured rates by different methods
190 are shown in Figure 1. Rates measured with the substrate tracer addition method (¹⁵NH₄⁺ and
191 ¹⁵NO₂⁻) outnumbered other methods globally but the product dilution method (¹⁵NO₂⁻ and ¹⁵NO₃⁻)
192 dominated in the Atlantic Ocean. The ammonia oxidation rates measured by different methods
193 have similar median values. However, the median nitrite oxidation rate measured by the ¹⁵NO₃⁻
194 dilution method is significantly higher than the rate measured by the ¹⁵NO₂⁻ addition method (200.3
195 vs 7.4 nmol N L⁻¹ d⁻¹). These comparisons, however, are between samples aggregated from
196 measurements taken at different sites. It is thus unclear whether the differences arise from
197 differences in the measurement approaches (e.g., in sensitivity) or in the sites where measurements
198 were made. A direct methods comparison is recommended for future exploration.
199



200

201 Figure 1. Distribution of different methods used to measure ammonia oxidation (a) and nitrite
202 oxidation (b). Others include ^{14}C incorporation and concentration change methods.

203

204 Incubations to measure nitrification rates have been conducted in polycarbonate and glass bottles,
205 exetainers and plastic bags. Seawater is directly transferred from the Niskin bottle into the
206 incubation containers to minimize temperature, oxygen and other perturbations. These incubation
207 containers are usually kept in an incubator with light filters to mimic the ambient temperature and
208 light conditions. After incubating for 3 hours to over 24 hours depending on the estimated
209 magnitude of nitrification rates, the incubation is terminated by filtering via GF/F or $0.22 \mu\text{m}$ filters
210 (e.g., Baer et al., 2017; Wan et al., 2019). The filtrate is then frozen at -20°C or -80°C until further
211 analysis on land. The incubation has also been terminated by subsampling and freezing without
212 filtration (e.g., Damashek et al., 2018). Alternatively, the incubation is preserved by adding
213 mercury chloride or zinc chloride (Kalvelage et al., 2013; Frey et al., 2020). This method allows
214 gas measurements like N_2O and N_2 production before nitrification analysis.

215



216 Various approaches have been developed to measure the N isotopes of NO_2^- and NO_3^- . For
217 example, 1) dissolved NO_2^- is extracted by formation of an azo dye. The resulting dye is filtered
218 onto precombusted GF/F or GF/C filters and its $^{15}\text{N}:^{14}\text{N}$ ratio is analyzed by elemental analyzer
219 isotope ratio mass spectrometry (Ward et al., 1982; Olson, 1981a). NO_3^- can be reduced to NO_2^-
220 by cadmium reduction and then extracted using the azo dye method described above. 2) Dissolved
221 NO_2^- is converted to Sudan-1 and Sudan-1 is collected via solid-phase extraction. The sample is
222 then purified by HPLC and derivatized before analysis by GC/MS (Clark et al., 2007). Similarly,
223 NO_3^- can be reduced to NO_2^- by cadmium prior to conversion to Sudan-1 for nitrogen isotope
224 analysis. 3) NO_2^- can be converted to N_2 with sulfamic acid and subsequently measured by isotope
225 ratio mass spectrometry (Dalsgaard et al., 2012; Bristow et al., 2016). 4) NO_2^- can also be
226 converted into N_2O by the azide method and subsequently measured by isotope ratio mass
227 spectrometry (Mcilvin and Altabet, 2005). The N isotopes of NO_2^- and NO_3^- can be measured via
228 the denitrifier method (Sigman et al., 2001; Weigand et al., 2016) where both NO_2^- and NO_3^- are
229 converted into N_2O . In addition, the $\delta^{15}\text{N}$ of NO_3^- alone can be measured using the denitrifier
230 method after removing NO_2^- with sulfamic acid (Granger and Sigman, 2009). The azide and
231 denitrifier methods require smaller sample volumes and offer a higher sensitivity of nitrogen
232 isotope detection.

233

234 Many factors may complicate the interpretation of rate measurements, e.g., isotope dilution by
235 regeneration of the ^{15}N -labeled substrates and stimulation of nitrification by substrate addition
236 (Lipschultz, 2008). For instance, the amount of tracer addition varied substantially from <10 nM
237 to $5 \mu\text{M}$, enriching the ambient pool by $<10\%$ to over 1000%. The excess addition of substrates
238 will likely enhance the nitrification rate, which will then reflect a potential rate instead of an in-
239 situ rate. In addition, the measurement of NO_2^- compared to $\text{NO}_2^- + \text{NO}_3^-$ could also lead to
240 variations in the estimates of the ammonia oxidation rates. Specifically, $^{15}\text{NO}_2^-$ produced from
241 $^{15}\text{NH}_4^+$ may be further oxidized to $^{15}\text{NO}_3^-$, especially when samples are low in NO_2^- concentration.
242 Ammonia oxidation rate may be underestimated if only $^{15}\text{NO}_2^-$ is measured instead of measuring
243 both $^{15}\text{NO}_2^-$ and $^{15}\text{NO}_3^-$ (Santoro et al., 2013; Peng et al., 2015). Therefore, NO_2^- carrier (to increase
244 the NO_2^- pool and trap the produced $^{15}\text{NO}_2^-$) may be added to the sample before incubation or both
245 NO_2^- and NO_3^- should be measured after incubation when ambient NO_2^- concentration is low. The
246 $^{15}\text{NO}_2^-$ isotope dilution method may overestimate ammonia oxidation rates because NO_2^- could



247 also be released from phytoplankton after assimilative nitrate reduction (Lomas and Lipschultz,
248 2006). These confounding factors may be difficult to quantify but worth recording and reporting
249 in publications for the sake of comparison among studies. In addition, a variety of approaches have
250 been applied to calculate nitrification rates. However, some methods correct for the impact of other
251 processes such as the uptake of the substrates or products of nitrification on rate estimates (e.g.,
252 Lipschultz et al., 1986; Santoro et al., 2010) while others do not (e.g., Dugdale and Goering,
253 1967).

254

255 Nitrification supported by organic N substrates like urea and cyanate has been observed in the Gulf
256 of Mexico (Kitzinger et al., 2018), Pacific (Santoro et al., 2017; Wan et al., 2021), off the east
257 coast of the United States (Laperriere et al., 2020; Tolar et al., 2017), and in the polar oceans
258 (Alonso-Saez et al., 2012; Shiozaki et al., 2021). The number of these observations remains limited
259 compared to ammonia oxidation. They can be included in future editions of the database (i.e., not
260 included in the current database) and their role in the marine N cycle deserves future investigations.
261

262 **Methods for quantifying ammonia oxidizers and nitrite oxidizers**

263 We summarize the primers used to quantify nitrifier abundance based on both functional genes
264 and 16S rRNA genes using quantitative PCR (qPCR) (Table 3). The cell abundance and biomass
265 can be subsequently estimated based on the gene abundance, number of genes per cell and specific
266 cell biomass (e.g., Kitzinger et al., 2020; Khachikyan et al., 2019). The oxidation of ammonia to
267 hydroxylamine is catalyzed by ammonia monooxygenase, which is partly encoded by the *amoA*
268 gene. Primers have been designed to quantify both bacterial and archaeal *amoA* genes (Rotthauwe
269 et al., 1997; Francis et al., 2005; Hornek et al., 2006; Wuchter et al., 2006; Beman et al., 2008;
270 Mosier and Francis, 2011; Sintès et al., 2013). Archaeal ammonia oxidizers are also separated into
271 different ecotypes including Water Column ecotypes A and B (WCA and WCB), which
272 preferentially inhabit the surface vs deep ocean, respectively, or high-ammonia concentration vs
273 low-ammonia concentration groups, which dominate in high ammonia vs low ammonia
274 concentration environments, respectively. The *nxrB* gene, which encodes the beta subunit of nitrite
275 oxidoreductase for nitrite oxidation, has been used to quantify *Nitrospira* (Pester et al., 2014).
276 However, no primers targeting *nxr* genes are available for other groups of nitrite oxidizers such as
277 *Nitrospina*, which is the dominant group of nitrite oxidizers in the ocean (Beman et al., 2013;



278 Pachiadaki et al., 2017). Primers have also been designed to quantify the 16S rRNA gene
 279 abundance of *Thaumarchaeota*, *Nitrospira*, and *Nitrospina* (Mincer et al., 2007; Graham et al.,
 280 2007). The abundance of nitrifiers can be useful for inferring and interpreting nitrification rates.
 281 In addition to qPCR, amplicon sequencing and quantitative metagenomics are also useful to
 282 determine the abundance of nitrifiers (Tolar et al., 2020; Lin et al., 2019; Satinsky et al., 2013) but
 283 these analyses are not included in the database.

284

285 Table 3. qPCR primers commonly used to quantify nitrifier abundance in the ocean.

Target	Name	Primer sequences (5'-3')	References
Gamma-bacterial <i>amoA</i>	amoA-1F	GGGGTTTCTACTGGTGGT	Rotthauwe et al., 1997
	amoA-2R	CCCCTCKGSAAAGCCTTCTTC	
	or amoA-r NEW	CCCCTCBGSAAAVCCTTCTTC	Hornek et al., 2006
Water Column ecotype A (WCA) archaeal- <i>amoA</i>	Arch-amoAFA	ACACCAGTTTGGYTACCWTC DGC	Beman et al., 2008; Francis et al., 2005
	Arch-amoAR	GCGGCCATCCATCTGTATGT	
Water Column ecotype A (WCB) archaeal- <i>amoA</i>	Arch-amoAFB	CATCCRATGTGGATTCCATCDTG	Beman et al., 2008; Francis et al., 2005
	Arch-amoAR	GCGGCCATCCATCTGTATGT	
Total archaeal- <i>amoA</i>	Arch-amoAF	STAATGGTCTGGCTTAGACG	Francis et al., 2005
	Arch-amoAR	GCGGCCATCCATCTGTATGT	
High-ammonia concentration archaeal- <i>amoA</i>	Arch-amoA-for	CTGAYTGGGCTGGACATC	Wuchter et al., 2006
	Arch-amoA-rev	TTCTTCTTTGTTGCCAGTA	
Low-ammonia concentration archaeal- <i>amoA</i>	Arch-amoA-for	CTGAYTGGGCTGGACATC	Wuchter et al., 2006 Sintes et al., 2013
	Arch-amoA-rev-New	TTCTTCTTCGTCGCCAATA	
<i>Thaumarchaeota</i> rRNA	16S GI_751F	GTCTACCAGAACAYGTTC	Mincer et al., 2007
		GI_956R	

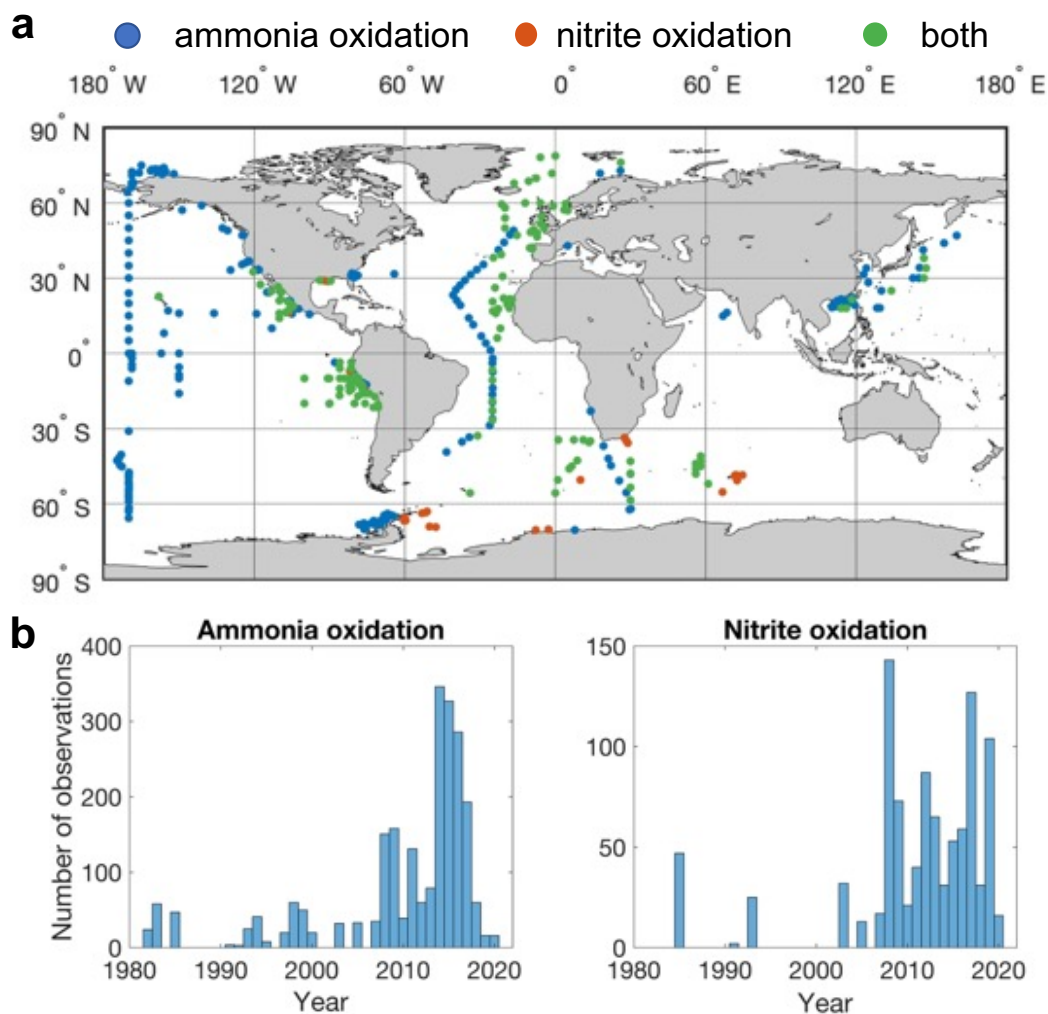


<i>nxr</i>	<i>nxB169F</i>	TACATGTGGTGGAACA	Pester et al., 2014
	<i>nxB638R</i>	CGGTTCTGGTTCRATCA	
<i>Nitrospira</i> 16S rRNA	<i>Nspra-675f</i>	GCGGTGAAATGCGTAGAKATCG	Graham et al., 2007
	<i>Nspra-746r</i>	TCAGCGTCAGRWAYGTTCCAGAG	
<i>Nitrospina</i> 16S rRNA	<i>NitSSU_130F</i>	GGGTGAGTAACACGTGAATAA	Mincer et al., 2007
	<i>NitSSU_282R</i>	TCAGGCCGGCTAAMCA	

286

287 Results and Discussion

288 Summary of the database



289

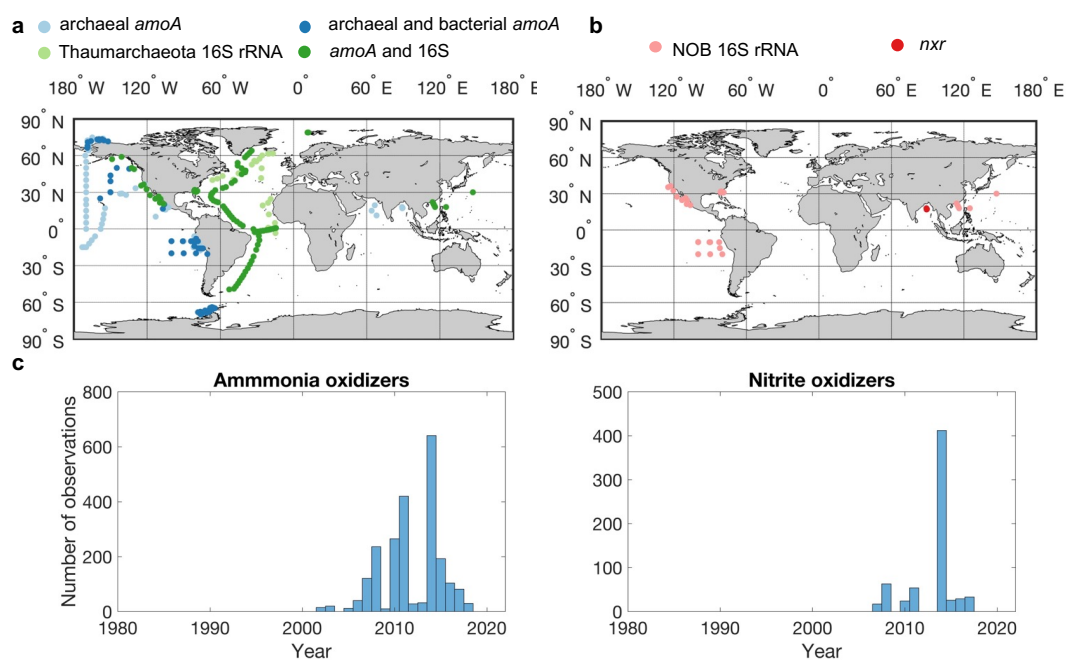


290 Figure 2. Map showing the distribution of sampling locations for nitrification rate measurements
291 (a) and the number of observations each year (b). Blue points: only ammonia oxidation is
292 measured; red points: only nitrite oxidation is measured. Green points: both ammonia oxidation
293 and nitrite oxidation are measured.

294

295 In total, there are 2393 and 1006 measurements of ammonia oxidation and nitrite oxidation,
296 respectively (Figure 2). Ammonia oxidation and nitrite oxidation have been concurrently measured
297 at 418 locations. The Pacific Ocean has the largest number of nitrification observations followed
298 by the Atlantic Ocean, Southern Ocean and Indian Ocean. Particularly, meridional transects across
299 ocean basins and biomes have been conducted in the North Pacific and Atlantic (Shiozaki et al.,
300 2016; Clark et al., 2008; Clark et al., 2022). Observations have recently expanded into oxygen
301 minimum zones (Beman et al., 2012; Beman et al., 2013; Frey et al., 2020; Frey et al., 2022; Peng
302 et al., 2015; Peng et al., 2016; Santoro et al., 2021; Sun et al., 2017) and polar oceans (Cavagna
303 et al., 2015; Shiozaki et al., 2019; Smith et al., 2022; Mduyana et al., 2022a and b; Mduyana et al.,
304 2020; Flynn et al., 2021). Nitrification rates are more frequently measured after 2010 (Figure 2b).

305



306



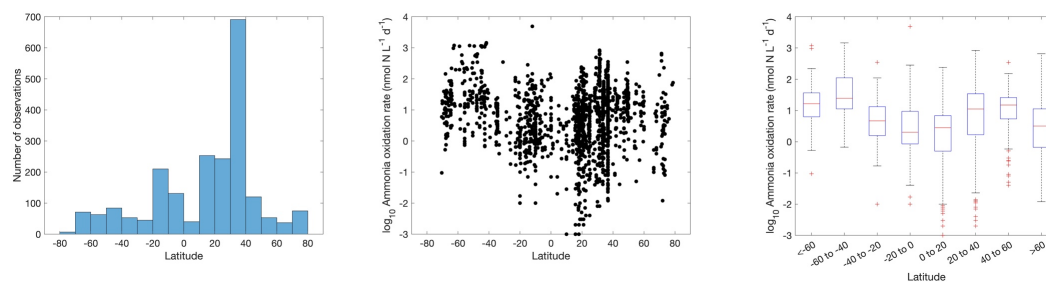
307 Figure 3. Maps showing the distribution of sampling locations for ammonia oxidizers (a) and
308 nitrite oxidizers (b), and the number of observations each year (c). (a) light blue points: only
309 archaeal *amoA* was quantified. Dark blue points: both archaeal and bacterial *amoA* genes were
310 quantified. Light green points: 16S rRNA gene of *Thaumarchaeota* was quantified; dark green
311 points: both archaeal *amoA* and 16S rRNA gene of *Thaumarchaeota* were quantified. (b) pink
312 points: 16S rRNA of nitrite oxidizers was quantified; red points: *nxr* gene of nitrite oxidizers was
313 quantified.

314

315 In total, there are 2187 and 631 measurements of ammonia oxidizer and nitrite oxidizer abundance,
316 respectively (Figure 3). Most of the nitrifier quantifications have been conducted in the tropical
317 and subtropical oceans (Figure 4a). Data are sparse in the central Pacific, Indian Ocean and
318 Southern Ocean (with the exception of the West Antarctic Peninsula). Both archaeal *amoA* and
319 16S rRNA genes of *Thaumarchaeota* were quantified on a transect across the Atlantic (Sintes et
320 al., 2016). There are far fewer observations of nitrite oxidizers compared to ammonia oxidizers.
321 Notably, there are only 27 observations of *nxr* genes. The number of the quantification of nitrifier
322 abundance starts to accumulate since 2002 (Figure 3c). Most of the observations of nitrite oxidizers
323 originates from one study where samples were collected in 2014 (Liu et al., 2018). Nitrification
324 rate and nitrifier abundance are sometimes determined at the same location, which allows us to
325 assess the relationship between biogeochemical rate and the abundance of functional groups (e.g.,
326 Peng et al., 2015; Shiozaki et al., 2019; Santoro et al., 2021).

327

328 Distribution of ammonia oxidation



329

330 Figure 4. Number of ammonia oxidation observations and ammonia oxidation rates within
331 latitudinal bands. For the boxplot in this figure and figures throughout the manuscript, the red line
332 in each box is the median. The bottom and top of each box are the 25th and 75th percentiles of the

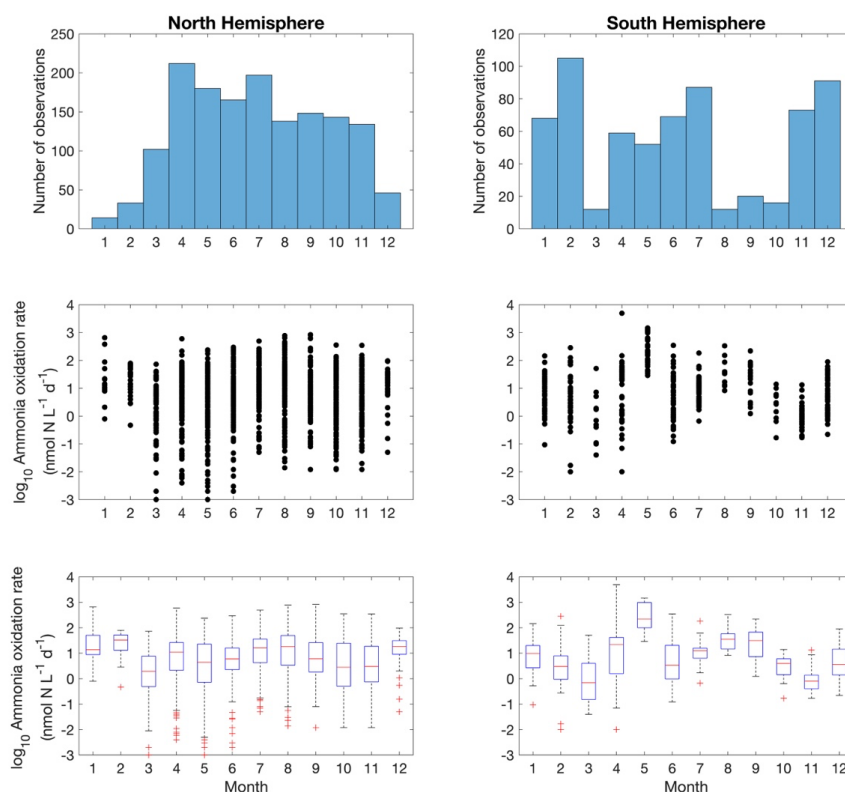


333 observations, respectively. The error bars represent 1.5 times the interquartile range away from the
334 bottom or top of the box, with red + signs showing outliers beyond that range.

335

336 A large number of observations exist for the tropical and temperate oceans (Figure 4), particularly
337 in the 30-40°N band where rates were measured in offshore waters of Georgia and California
338 (Tolar et al., 2020; Liu et al., 2018). Ammonia oxidation rates vary from <math><0.01</math> to over 1000 nmol
339 340 ammonia oxidation rates. In contrast, Clark et al. (2022) found higher ammonia oxidation rates in
341 the southern hemisphere along the north-south transect in the Atlantic Ocean. This latitudinal
342 pattern is hypothesized to be explained by the difference in the supply of dissolved organic
343 nitrogen (DON) by lateral transport into the gyre interior from the eastern boundary upwelling
344 (Clark et al., 2022). The stimulation of ammonia oxidation rates by a lateral DON supply has also
345 been observed in the Western Pacific (Xu et al., 2018).

346



347

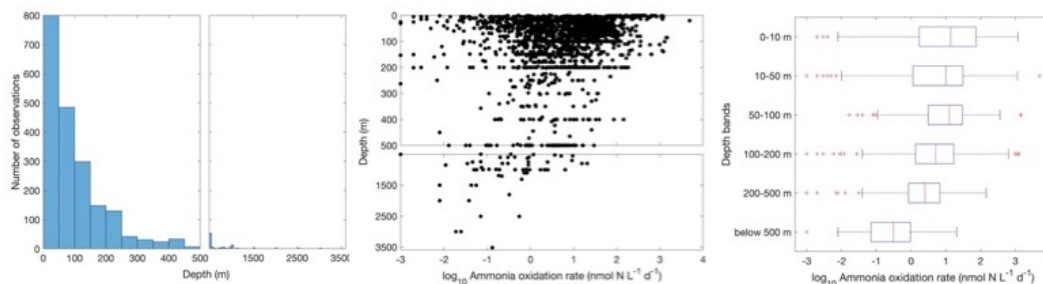


348 Figure 5. Monthly variation of ammonia oxidation observations and ammonia oxidation rates
349 divided into observations taken in the Northern Hemisphere (left panels) and Southern Hemisphere
350 (right panels).

351

352 More ammonia oxidation measurements were conducted in summer in both hemispheres (Figure
353 5) which is likely due to the more challenging weather conditions in winter for field explorations.
354 The northern hemisphere has more observations compared to the southern hemisphere. Although
355 no clear seasonal pattern is apparent for ammonia oxidation rates at a global scale, seasonal
356 variation in ammonia oxidation has been seen at time-series stations near and offshore of
357 California (Ward, 2005; Tolar et al., 2020; Laperriere et al., 2020). In addition, ammonia oxidation
358 showed a substantial seasonal pattern in the polar ocean with higher rates observed in the NH_4^+ -
359 enriched dark winter season (Baer et al., 2017; Mduyana et al., 2020; Mduyana et al., 2022b).

360



361

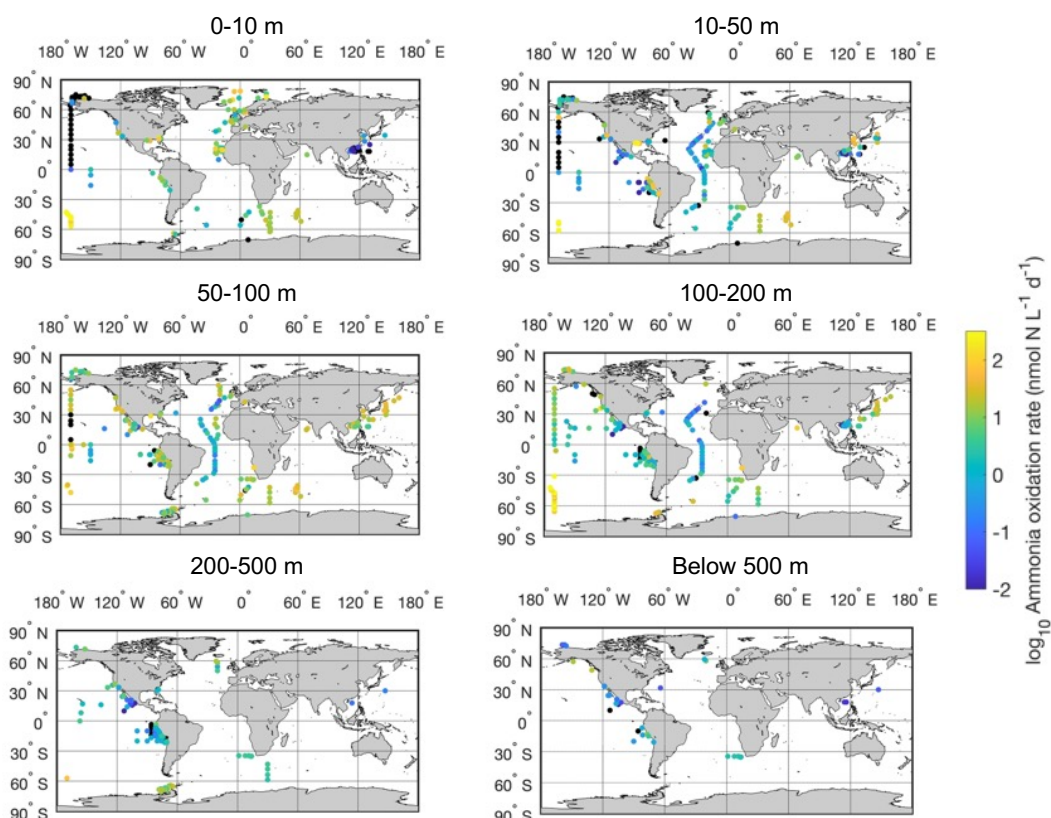
362 Figure 6. Vertical variation of ammonia oxidation observations and ammonia oxidation rates.

363

364 Most of the ammonia oxidation rate measurements were made shallower than 500 m, accounting
365 for ~96% of the total measurements (Figure 6). Ammonia oxidation rates often reach a maximum
366 near the base of the euphotic zone or in the 50-100 m layer before decreasing with depth below
367 the euphotic zone. Although nitrification is thought to be inhibited by light, high ammonia
368 oxidation rates $>100 \text{ nmol N L}^{-1} \text{ d}^{-1}$ have been observed within the euphotic zone (Raes et al.,
369 2020; Bianchi et al., 1997), suggesting complex regulation of nitrification in the surface ocean.
370 This complicates the interpretation of the source of NO_3^- in the euphotic zone and further the NO_3^- -
371 supported new production (Diaz and Raimbault, 2000; Yool et al., 2007; Grundle et al., 2013;
372 Mduyana et al. 2020).



373



374

375 Figure 7. Spatial distribution of ammonia oxidation rates in six depth intervals in the global ocean.

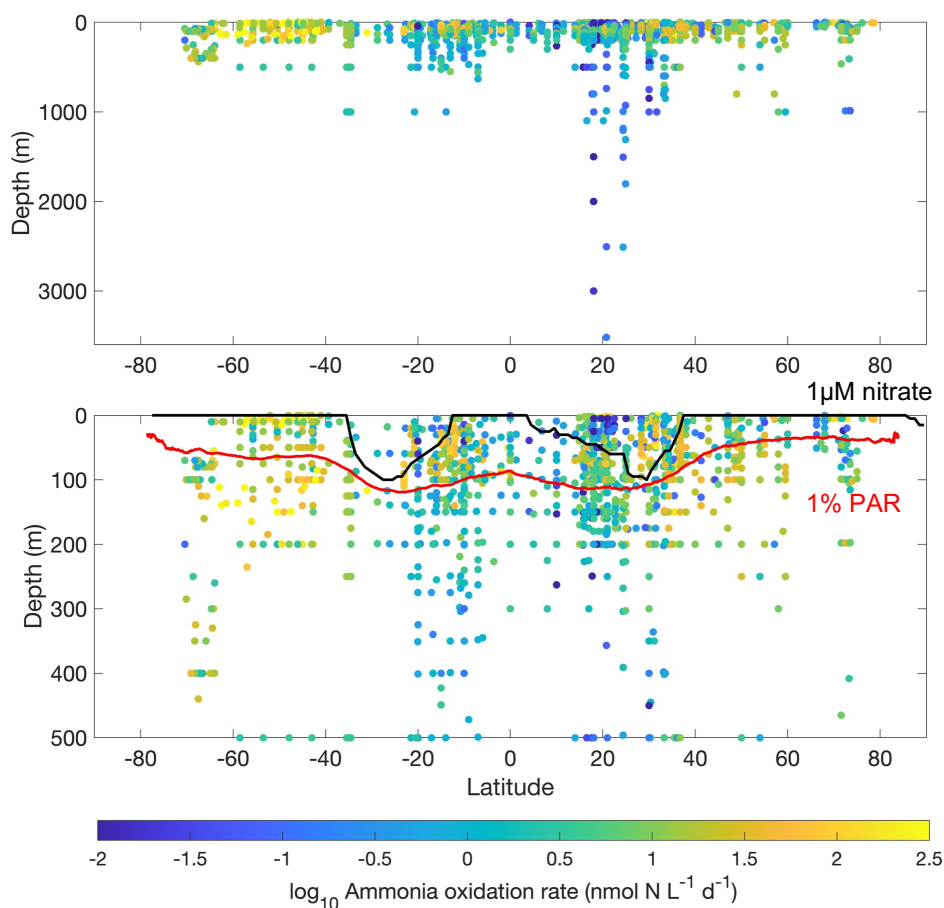
376 Locations with rates below the detection limit are shown in the black circles.

377

378 There is a large spatial and vertical variation in ammonia oxidation rates (Figure 7). Some hotspots
379 with rates $>100 \text{ nmol N L}^{-1} \text{d}^{-1}$ include the subpolar North Atlantic (Clark et al., unpublished),
380 Southern Ocean (Mdutyana et al., 2020), and coastal waters off California and Georgia (Tolar et
381 al., 2020; Liu et al., 2018). Particularly, there are extremely high ammonia oxidation rates >1000
382 $\text{nmol N L}^{-1} \text{d}^{-1}$ observed in the surface Pacific Southern Ocean (Raes et al., 2020), deserving further
383 studies to confirm this pattern. In contrast, some low rates $<0.01 \text{ nmol N L}^{-1} \text{d}^{-1}$ or rates below the
384 detection limit are found in the surface sunlit North Pacific, which is likely caused by the light
385 inhibition on nitrifiers, and nitrifiers' competition with phytoplankton for NH_4^+ in well-lit areas
386 (Smith et al., 2014). For example, peak ammonia oxidation rates are often found in regions/depths



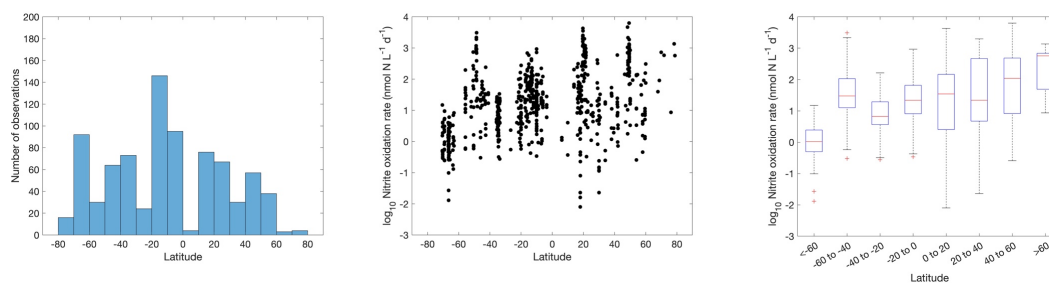
387 where NO_3^- is present or light levels are low such that competition of nitrifiers with phytoplankton
388 for NH_4^+ diminishes (Figure 8; Wan et al., 2021). Additionally, low rates are found in oxygen-
389 depleted waters of the eastern tropical Pacific where ammonia oxidation is likely limited by
390 oxygen availability (Peng et al., 2016)
391



392
393 Figure 8. Latitudinal and vertical distribution of ammonia oxidation rates. The lower panel shows
394 data from the top 500 m. The climatological depths of the euphotic zone (1% PAR) obtained from
395 MODIS satellite observations and 1 μM nitrate obtained from World Ocean Atlas 2018 (García et
396 al., 2019) are shown by the red line and black lines, respectively.
397



398 Distribution of nitrite oxidation



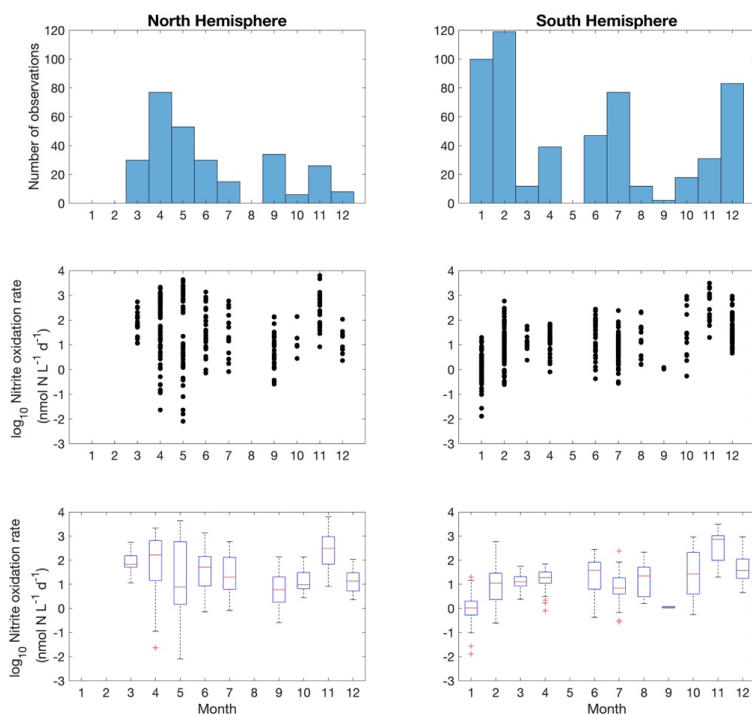
399

400 Figure 9. Number of nitrite oxidation observations and nitrite oxidation rates within latitudinal
401 bands.

402

403 Similar to ammonia oxidation, the majority of the nitrite oxidation observations were conducted
404 in the tropical and subtropical oceans (Figure 9), particularly in the eastern tropical Pacific oxygen
405 minimum zones (Ward et al., 1989; Peng et al., 2015; Kalvelage et al., 2013; Santoro et al., 2021).
406 Recent observations extended into the Southern Ocean (Cavagna et al., 2015; Mdotyana et al.,
407 2020; Mdotyana et al., 2022a; Flynn et al., 2021). The rates vary from 0.01 to >1000 $\text{nmol N L}^{-1} \text{d}^{-1}$
408 d^{-1} with a median value at 15.9 ± 10.7 $\text{nmol N L}^{-1} \text{d}^{-1}$. Nitrite oxidation rates seem to increase from
409 the southern hemisphere to northern hemisphere. The lowest median rates were found in the
410 Southern Ocean south of 60°S , which is hypothesized to be regulated by low iron availability
411 (Mdotyana et al., 2022a). Overall, more measurements of nitrite oxidation over a large spatial scale
412 are desired to resolve the latitudinal distribution of nitrite oxidation rates.

413



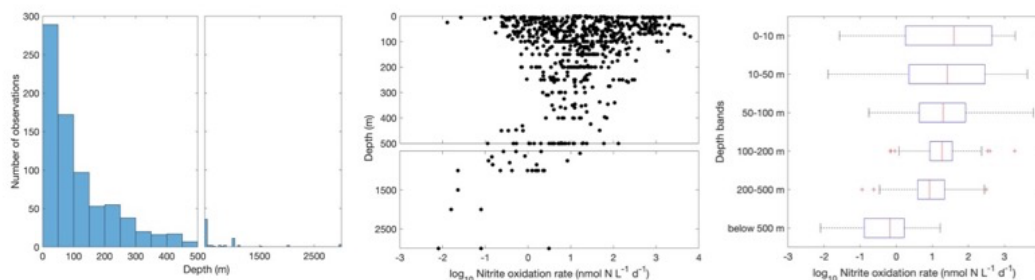
414

415 Figure 10. Monthly variation of nitrite oxidation observations and nitrite oxidation rates.

416

417 Nitrite oxidation measurements are limited in winter in the northern hemisphere (Figure 10). No
 418 clear seasonal pattern is found for nitrite oxidation rates at a global scale, except for some of the
 419 lowest rates detected in January in the Southern Ocean (austral summer). In addition to iron
 420 limitation, light inhibition and competition with phytoplankton for nitrite during the growing
 421 season may be important factors driving these low rates. Unlike ammonia oxidation, there is no
 422 time-series study of nitrite oxidation to show its seasonal variations.

423



424

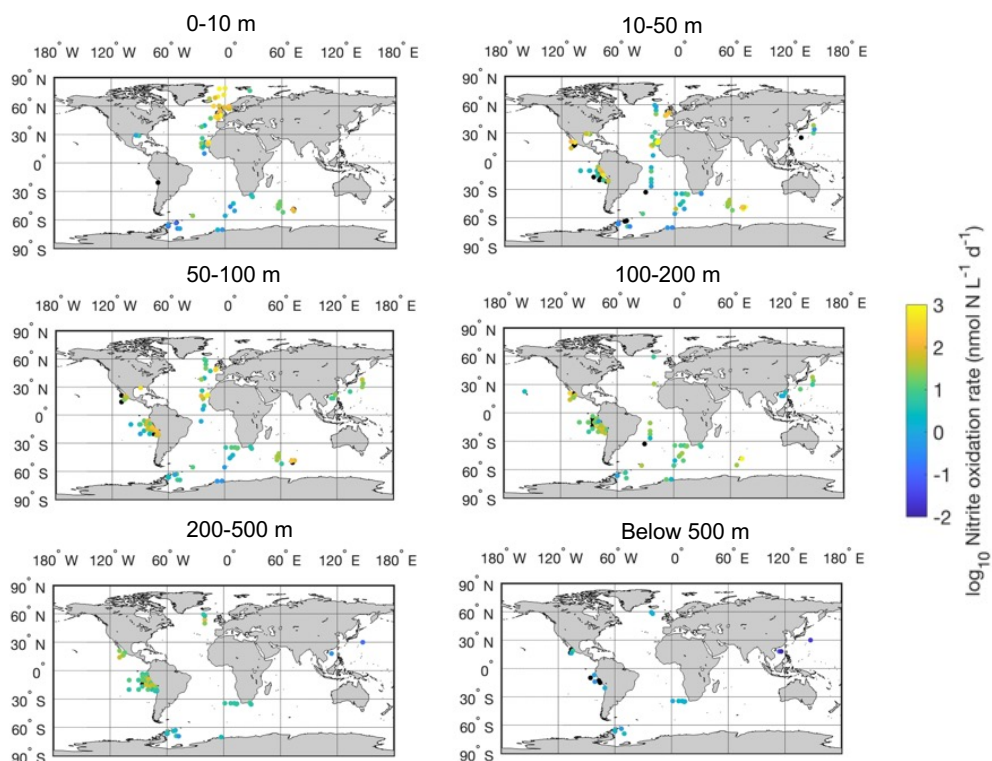


425 Figure 11. Vertical variation of nitrite oxidation observations and nitrite oxidation rates.

426

427 Most of the nitrite oxidation rates were also measured at depths shallower than 500 m, accounting
428 for ~94% of the total measurements (Figure 11). There is a large spatial variation in the nitrite
429 oxidation observations and rates (Figure 12). Observations are lacking in the central Pacific Ocean
430 and Indian Ocean outside of the oxygen minimum zones. Nitrite oxidation rates decrease with
431 depth. Globally, the highest median nitrite oxidation rates were found in the surface water (0-10
432 m layer), which is mainly attributed to the high surface rates observed over the United Kingdom
433 shelves, subpolar North Atlantic and Mauritanian upwelling system (Figure 12; Clark et al.,
434 unpublished; Clark et al., 2016). After removing these high surface nitrite oxidation rates, the depth
435 profiles of nitrite oxidation often show a subsurface maximum that is slightly deeper than the
436 subsurface maximum of ammonia oxidation (Figure 13). This difference may be related to the
437 higher sensitivity of nitrite oxidizers/nitrite oxidation to light (Wan et al., 2021; Olson, 1981b).
438 Interestingly, some deep peaks of nitrite oxidation rates have been found in the oxygen-depleted
439 waters in the oxygen minimum zones (Peng et al., 2015; Babbín et al., 2020; Ward et al., 1989;
440 Beman et al., 2013). These high rates stand out in depths below the 1 μM nitrate threshold and
441 above the 1% PAR level between 20°N and 20°S (Figure 14). Many hypotheses (Sun et al., 2023)
442 have been proposed to explain the observed “anaerobic” nitrite oxidation, including alternative
443 oxidants like iodate (Babbín et al., 2017), distinct nitrite oxidizers that are only present in the
444 OMZs and adapted to the low oxygen conditions (Sun et al., 2021), nitrite dismutation ($2\text{H}^+ +$
445 $5\text{NO}_2^- \rightarrow \text{N}_2 + 3\text{NO}_3^- + \text{H}_2\text{O}$; van de Leemput et al., 2011; Babbín et al., 2020; Tracey et al., 2022),
446 and oxygen intrusions (Buchanan et al., 2023). Whether nitrite oxidation is truly anaerobic and
447 how nitrite oxidation is sustained in oxygen depleted waters remain to be determined.

448

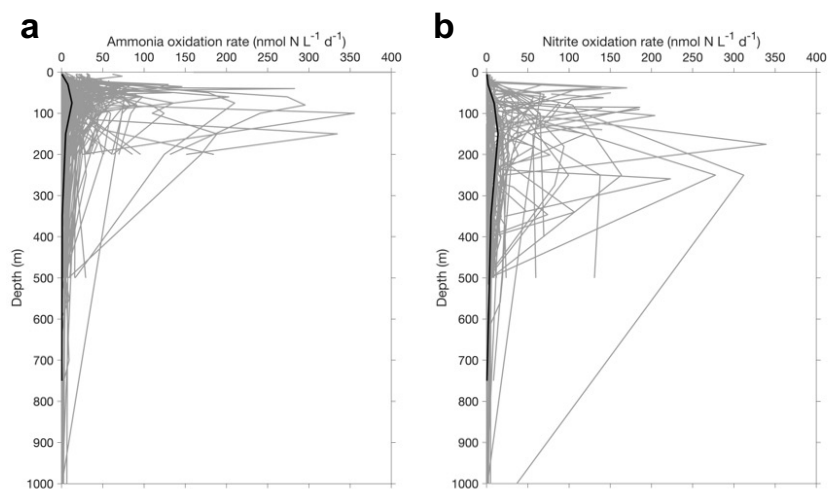


449

450 Figure 12. Spatial distribution of nitrite oxidation rates in six depth intervals in the global ocean.

451 Locations with rates below the detection limit are shown in the black circles.

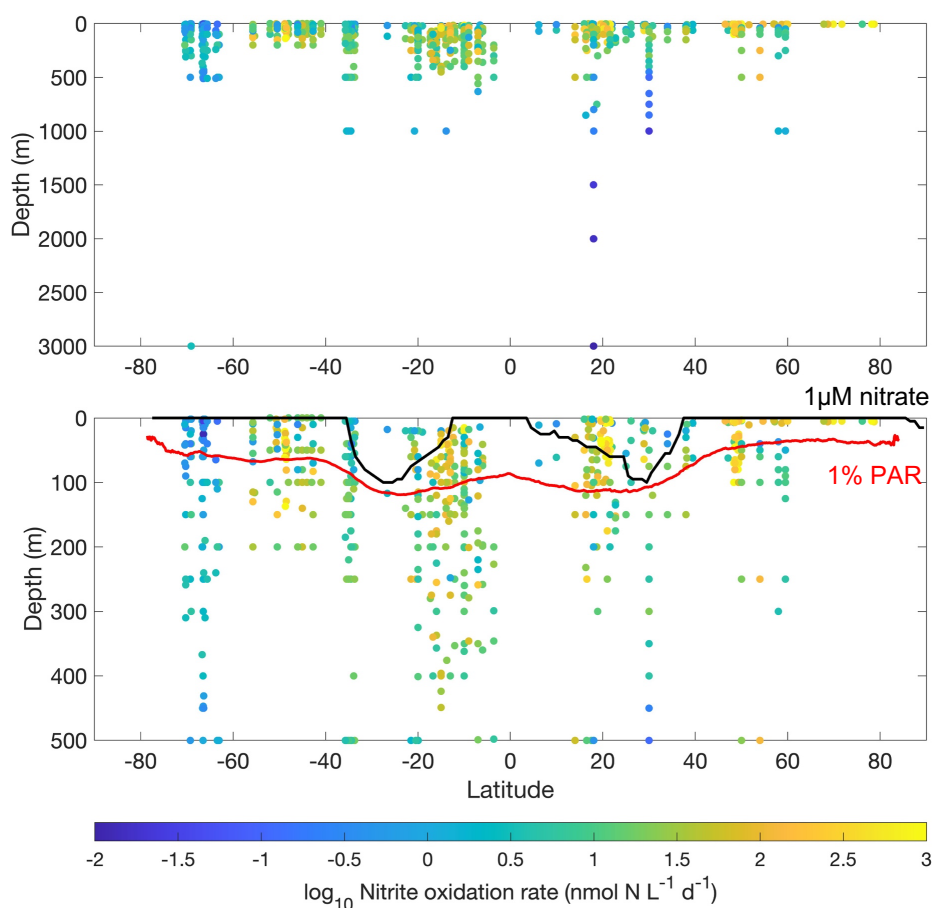
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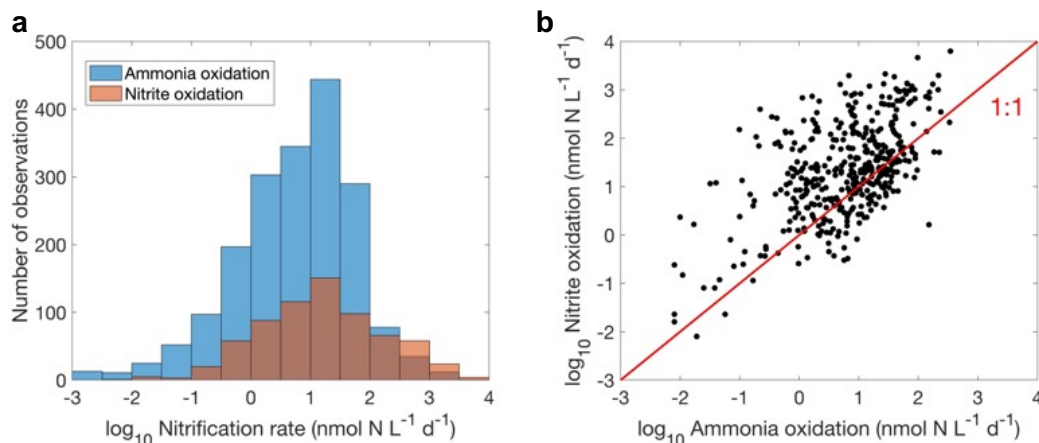
453



454 Figure 13. Depth profiles of ammonia oxidation (a) and nitrite oxidation (b) in the top 1000 m.
455 Only depth profiles with five or more measurements are included in this figure. The median
456 profiles of ammonia oxidation and nitrite oxidation are shown in thick black lines, showing the
457 maximum of nitrite oxidation deeper than the maximum of ammonia oxidation.
458



459
460 Figure 14. Latitudinal and vertical distribution of nitrite oxidation rates. The lower panel shows
461 data from the top 500 m. The climatological depth of the euphotic zone (1% PAR) and 1 μM nitrate
462 are shown by the red and black lines respectively.
463



464

465 Figure 15. Comparison between ammonia oxidation and nitrite oxidation. (a) Histogram of both
466 rates globally. (b) Relationship between ammonia oxidation and nitrite oxidation measured at the
467 same locations and time ($y=0.62*x+0.82$, $r=0.54$, $p<0.01$).

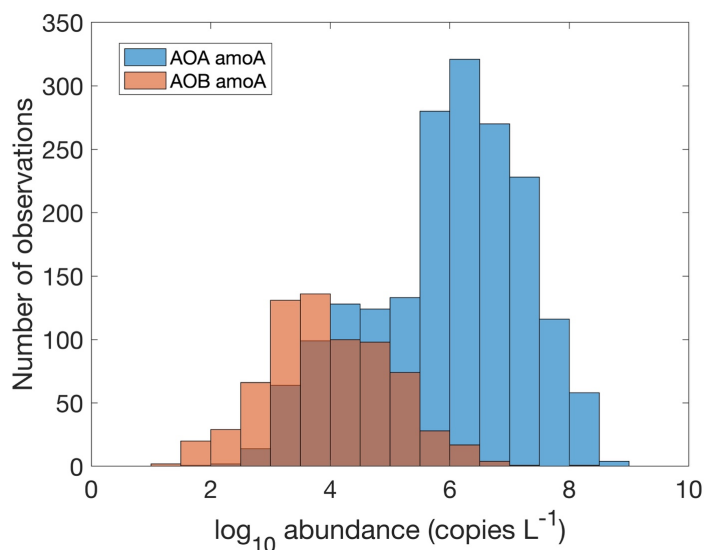
468

469 Overall, there are fewer nitrite oxidation rate measurements compared to ammonia oxidation
470 measurements (Figure 15a). Ammonia oxidation and nitrite oxidation are generally of similar
471 magnitude (Figure 15b), leading to the low concentration of NO_2^- in most of the ocean. However,
472 ammonia oxidation and nitrite oxidation could be decoupled. For example, higher ammonia
473 oxidation rates than nitrite oxidation rates (Lomas and Lipschultz, 2006) and competition between
474 ammonia oxidation and phytoplankton ammonium assimilation (Zakem et al. 2018) may both
475 partly explain the presence of the primary nitrite maximum. The median nitrite oxidation rate is
476 higher than the median ammonia oxidation rate (15.9 vs 7.7 $\text{nmol N L}^{-1} \text{d}^{-1}$), which may be related
477 to nitrite production pathways from urea and cyanate oxidation in addition to ammonia oxidation
478 (Wan et al., 2022; Kitzinger et al., 2018). Consistently, when comparing ammonia oxidation and
479 nitrite oxidation rates measured at the same locations and same time, nitrite oxidation rates are
480 mostly higher (Figure 15b). Mechanisms driving the decoupling of ammonia oxidation and nitrite
481 oxidation deserve further investigations.

482



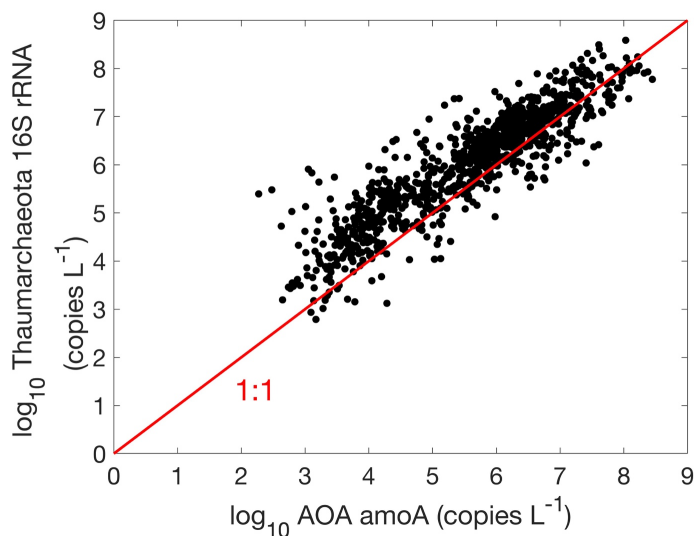
483 Distribution of ammonia oxidizers



484

485 Figure 16. Comparison between the gene abundance of AOA *amoA* and AOB *amoA*.

486



487

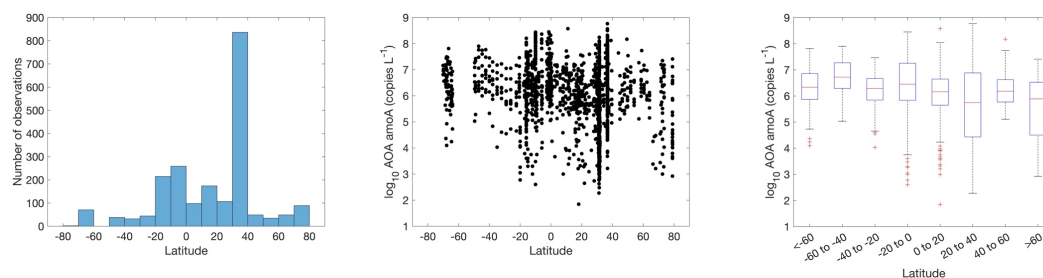
488 Figure 17. Comparison between archaeal *amoA* and *Thaumarchaeota* 16S rRNA gene abundances

489 ($y=0.78*x+1.66$, $r=0.9$, $p<0.01$).

490

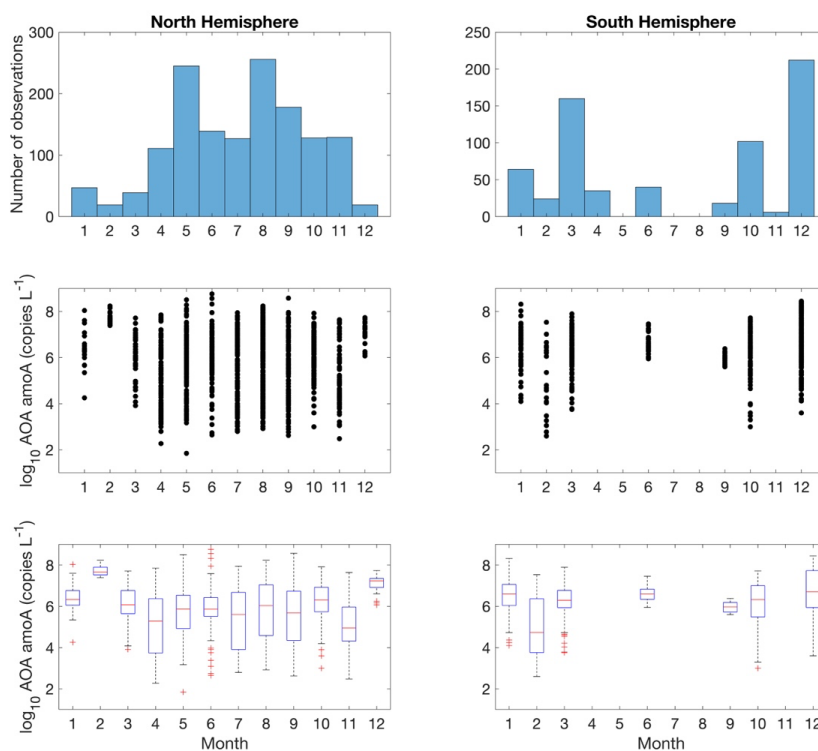


491 There are 1893, 892, 1073 measurements of the abundance of archaeal *amoA* gene, bacterial *amoA*
492 and 16S rRNA of *Thaumarchaeota*, respectively. In addition, 1204 and 1101 measurements were
493 separately conducted for water column ecotype A (WCA) *amoA* and water column ecotype B
494 (WCB) *amoA*. The AOA *amoA* abundance with median of 1.34×10^6 copies L^{-1} is substantially
495 higher than AOB *amoA* gene abundance with median of 7.96×10^3 copies L^{-1} (Figure 16),
496 confirming the dominance of archaeal ammonia oxidizers in the ocean. We also found that
497 *Thaumarchaeota* 16S rRNA gene abundance positively correlates with but slightly outnumbers
498 the *amoA* gene abundance (Figure 17). This may suggest that not all the *Thaumarchaeota* contain
499 the *amoA* genes to oxidize NH_4^+ or some organisms containing *amoA* genes (such as the
500 *Nitrosopumilus*-like group) may have been missed due to primer bias (Sintes et al., 2016; Hiraoka
501 et al., preprint), Since archaeal *amoA* genes have the largest number of observations and better
502 represent ammonia oxidation capability, we will use it to show the spatial and vertical distribution
503 of ammonia oxidizer abundance.
504



505
506 Figure 18. Number of observations of ammonia oxidizers and the abundance of ammonia oxidizers
507 within latitudinal bands.

508
509 The eastern Pacific Ocean and Atlantic Ocean have the majority of the observations for ammonia
510 oxidizers, particularly in the 30-40°N band where ammonia oxidizers were measured in the coastal
511 waters off California and Georgia (Liu et al., 2018; Tolar et al., 2020). In contrast, observations in
512 the Indian Ocean and Southern Ocean are scarce. The AOA *amoA* gene abundance varies from a
513 few copies per liter in the surface ocean to over 10^8 copies L^{-1} in the subsurface of equatorial
514 Atlantic. There is no clear latitudinal trend in the abundance of ammonia oxidizers.
515



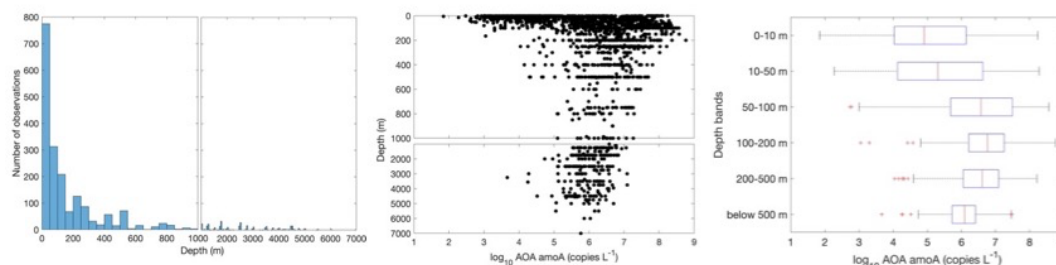
516

517 Figure 19. Monthly variation of the observation and abundance of ammonia oxidizers.

518

519 There are substantially more observations in the northern hemisphere than the southern
520 hemisphere. We do not see a clear seasonal trend in nitrifier abundance due to the large monthly
521 variation. A time-series study in the Monterey Bay shows that seasonality can be observed for the
522 top 200 m while the overall community of ammonia oxidizers was stable at 500 m (Tolar et al.,
523 2020). In addition, mid-summer peaks in *Thaumarchaeota* abundance have been observed at the
524 coast off Georgia (Hollibaugh et al., 2013). More time-series studies with high-frequency sampling
525 would be useful for characterizing the response of the nitrifier community to seasonal changes in
526 environmental drivers.

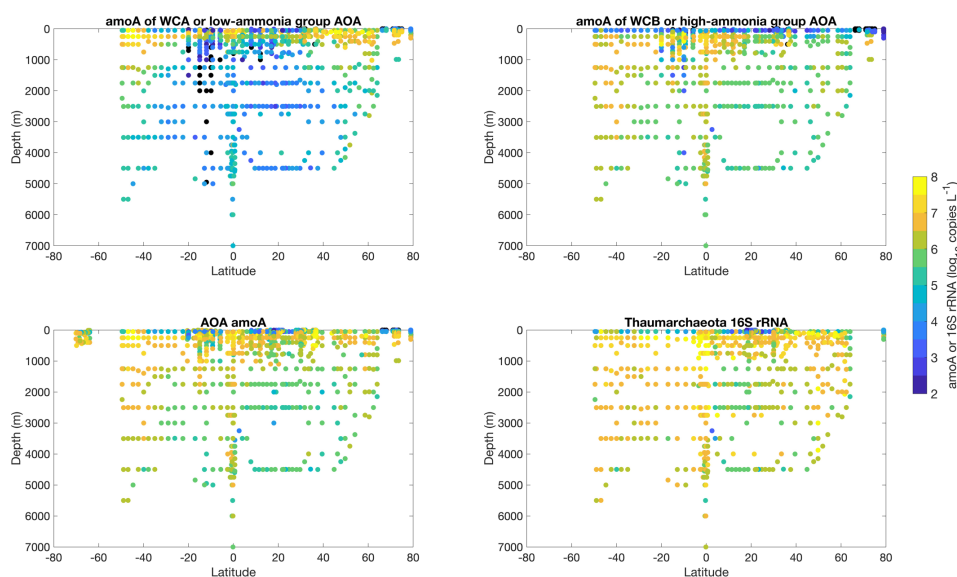
527



528

529 Figure 20. Vertical distribution of archaeal *amoA* observations and archaeal *amoA* gene
530 abundance.

531



532

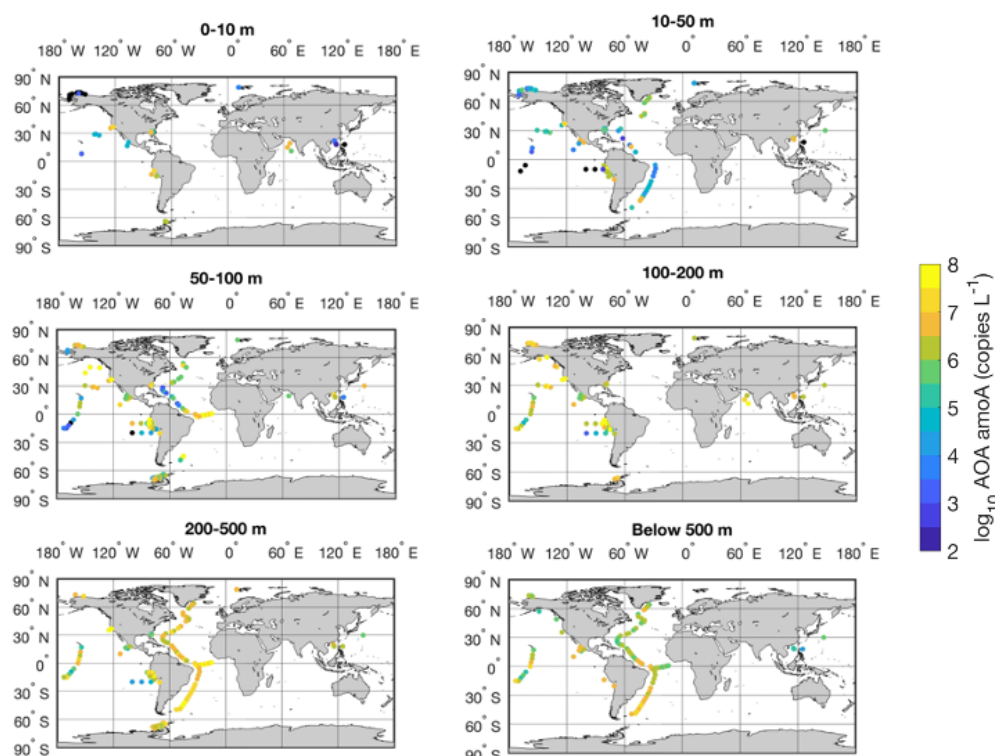
533 Figure 21. Vertical distribution of archaeal *amoA* gene abundance and 16S rRNA of
534 *Thaumarchaeota* across the latitudinal gradient. WCA and high-ammonia concentration groups
535 are shown together while WCB and low-ammonia concentration groups are shown together.

536

537 Most of the abundance measurements of ammonia oxidizers were made in the top 1000 m (Figure
538 20). Median ammonia oxidizer abundance increases from $\sim 10^5$ copies L^{-1} in the 0-10 m depth layer
539 to $\sim 10^7$ copies L^{-1} in the 100-200 m layer, then decreases with depth and remains relatively
540 constant at $\sim 10^6$ copies L^{-1} in the deep ocean below 500 m depth. The archaeal *amoA* is sometimes
541 quantified separately for two ecotypes including water column groups A and B. Water column



542 group A dominates the upper 200 meter while water column group B is more abundant in the
543 mesopelagic and bathypelagic deep ocean below 500 m, likely reflecting their different affinities
544 for NH_4^+ (Beman et al., 2008; Sintes et al., 2016). The vertical distribution of ammonia oxidizers
545 is similar to the vertical distribution of ammonia oxidation rates (Figure 13).
546



547
548 Figure 22. Spatial distribution of *amoA* gene in six depth intervals in the global ocean. Locations
549 with abundance below the detection limit are shown in the black circles.

550
551 There is a large spatial variation in the abundance of ammonia oxidizers (Figure 22). High
552 abundances are found in the tropical Atlantic and eastern tropical Pacific where upwelling drives
553 high rates of marine primary production. In contrast, some of the lowest abundances of ammonia
554 oxidizers are found in the South China Sea and oligotrophic subtropical Pacific. Therefore, the
555 distribution of marine productivity and organic matter production and export may play an
556 important role in regulating the distribution of ammonia oxidizers because ammonia oxidizers rely
557 on the supply of NH_4^+ , which is generated by of organic matter decomposition.



558

559 **Distribution of nitrite oxidizer abundance**

560 There are only seven studies available reporting the abundance of nitrite oxidizers in the ocean.

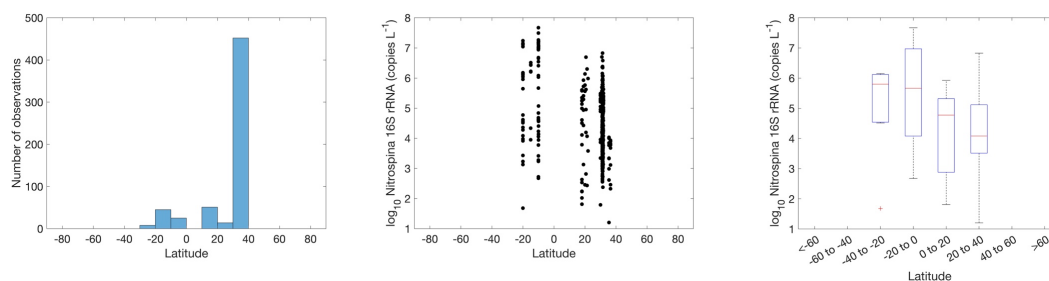
561 One study used the *nxr* marker gene and the other six studies used 16S rRNA gene of either

562 *Nitrospina* or *Nitrospira*. Since *Nitrospina* is the dominant nitrite oxidizer in the ocean (Beman et

563 al., 2013; Pachiadaki et al., 2017) and accounts for most of the observations, we use it to show the

564 distribution of nitrite oxidizers.

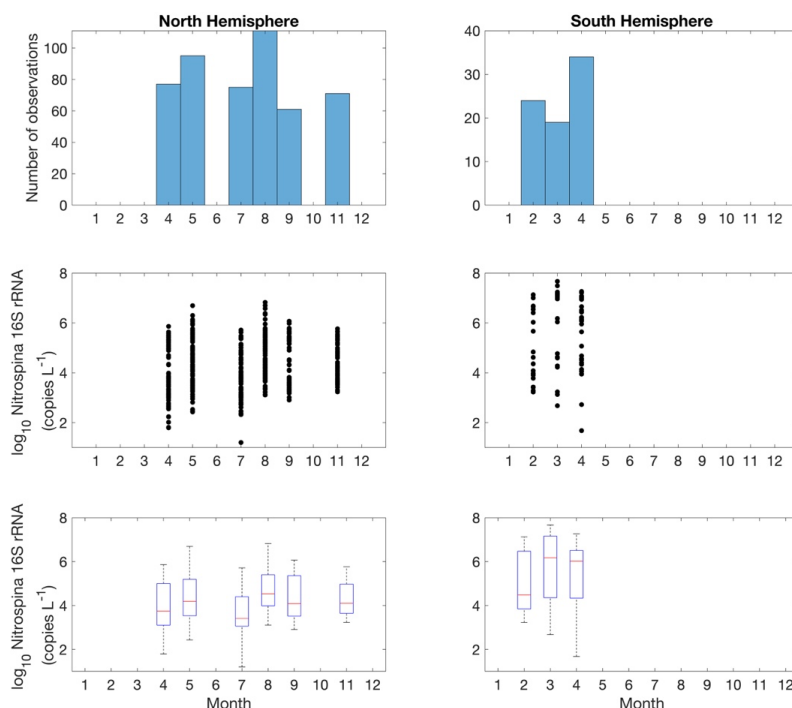
565



566

567 Figure 23. Number of observations and abundance of *Nitrospina* within latitudinal bands.

568



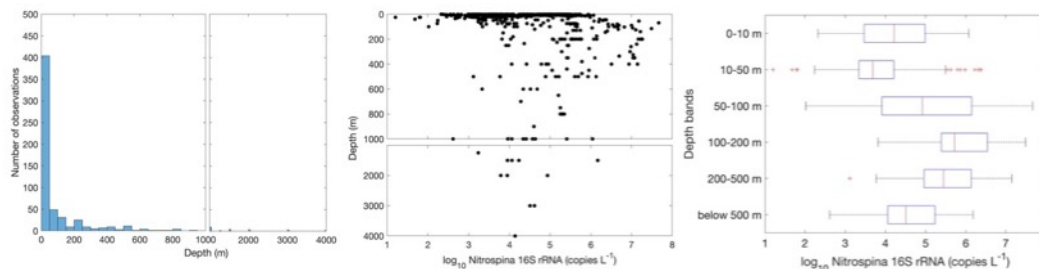
569

570 Figure 24. Monthly variation of observations and abundance of *Nitrospina*.

571

572 Quantification of nitrite oxidizers using the 16S rRNA gene is limited to a few locations between
 573 40°N to 40°S including the coastal waters off California and Georgia, the eastern tropical South
 574 Pacific, Bay of Bengal, and western Pacific (Figure 23). The number of observations is dominated
 575 by one study conducted near the coast of Georgia (Liu et al., 2018). The highest abundance of 4.68
 576 $\times 10^7$ copies L^{-1} was found in the eastern tropical South Pacific. No clear latitudinal or seasonal
 577 trend can be determined based on the limited number of observations (Figures 23-24).

578



579

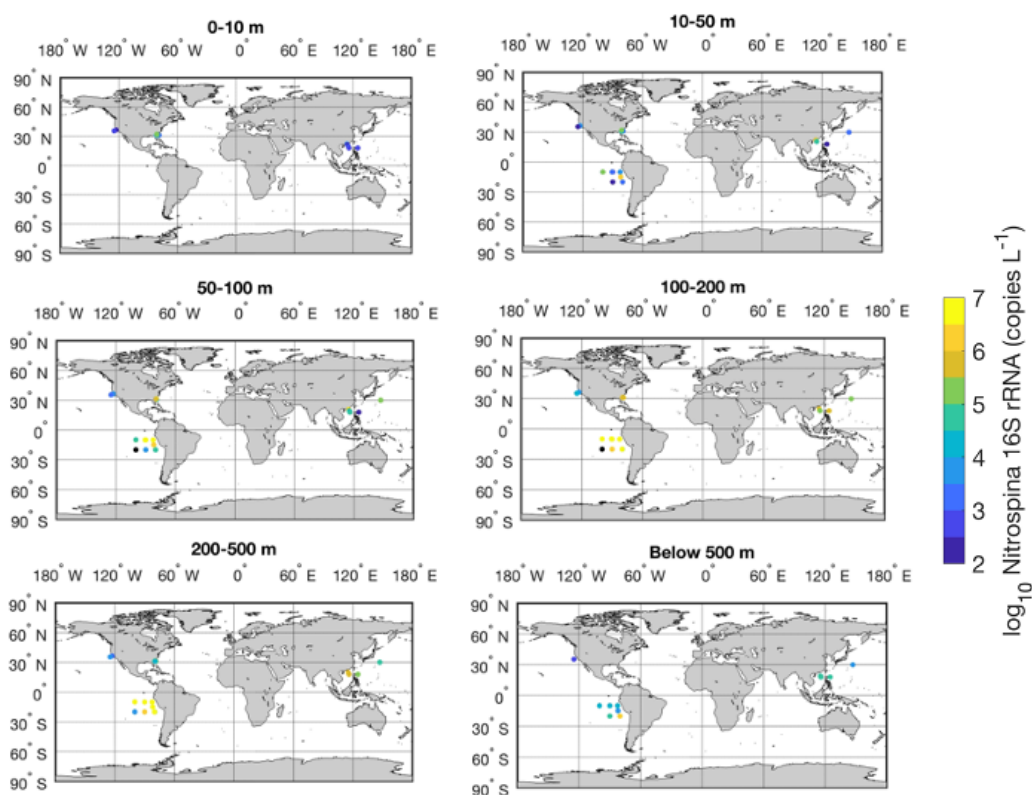


580 Figure 25. Vertical distribution of *Nitrospina* observations and gene abundance.

581

582 The vertical distribution of nitrite oxidizers resembles the vertical distribution of ammonia
583 oxidizers: increases from $\sim 10^4$ copies L^{-1} in the surface 0-10 m depth layer to a maximum of $\sim 10^6$
584 copies L^{-1} in the 100-200 m layer, then decreases to $\sim 10^{4.5}$ copies L^{-1} in the deep ocean below 500
585 m (Figures 25-26). However, data below 500 m are insufficient to describe the distribution of
586 nitrite oxidizers in the deep ocean. The vertical distribution of nitrite oxidizers qualitatively
587 matches the vertical distribution of nitrite oxidation rates (Figure 13).

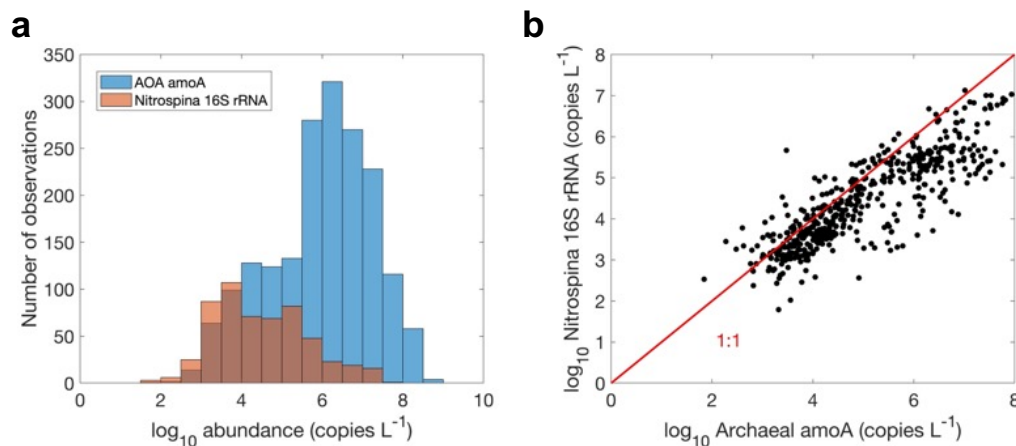
588



589

590 Figure 26. Spatial distribution of *Nitrospina* in six depth intervals in the global ocean. Locations
591 with abundances below the detection limit are shown in the black circles.

592



593

594 Figure 27. Comparison between the abundance of the archaeal *amoA* gene and *Nitrospina* 16S
595 rRNA gene ($y=0.68*x+1$, $r=0.85$, $p<0.01$).

596

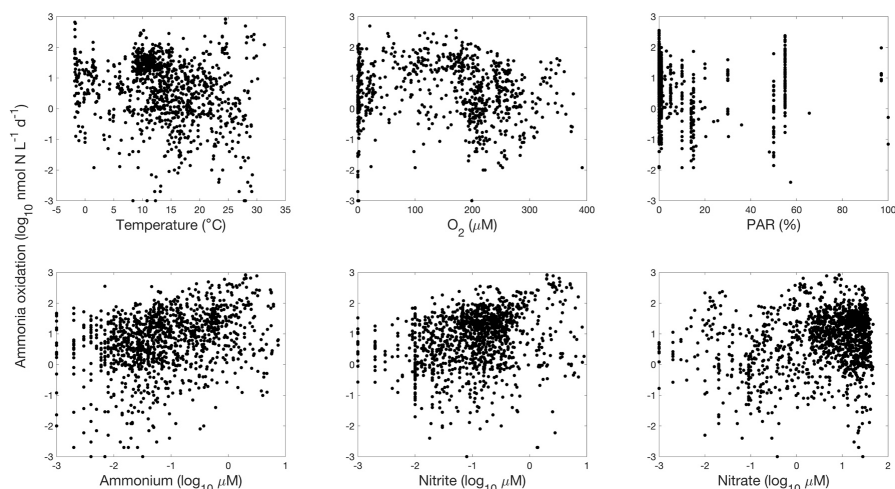
597 When comparing ammonia oxidizers with nitrite oxidizers, median abundance of ammonia
598 oxidizers of 1.34×10^6 copies L^{-1} is approximately two orders of magnitude higher than the median
599 nitrite oxidizer of 2.14×10^4 copies L^{-1} . The difference in their abundance has been predicted by
600 the relative biomass yields and cell quotas (Zakem et al., 2018; Zakem et al., 2022) and
601 alternatively is explained by the difference in the mortality/loss rates between AOA and *Nitrospina*
602 (Kitzinger et al., 2020). In addition, there is a positive relationship between the abundance of
603 ammonia oxidizers and nitrite oxidizers (Figure 27) as previously shown in observations from the
604 Pacific (Santoro et al., 2019), indicating their coexistence under most conditions.

605

606 Environmental controls on nitrification rates and the abundance of nitrifiers

607 We compared the measured nitrification rates and nitrifier abundance with concurrently measured
608 or available environmental factors including temperature, oxygen, light, and N concentration
609 (NH_4^+ , NO_2^- , NO_3^-) to assess the environmental controls on nitrification and nitrifiers (Figures 28-
610 31). We acknowledge that nitrification rates and nitrifier abundance are regulated by multiple
611 environmental factors, which may not be revealed by the simple correlation analysis with
612 individual factors. The new database will facilitate more sophisticated future analyses.

613



614

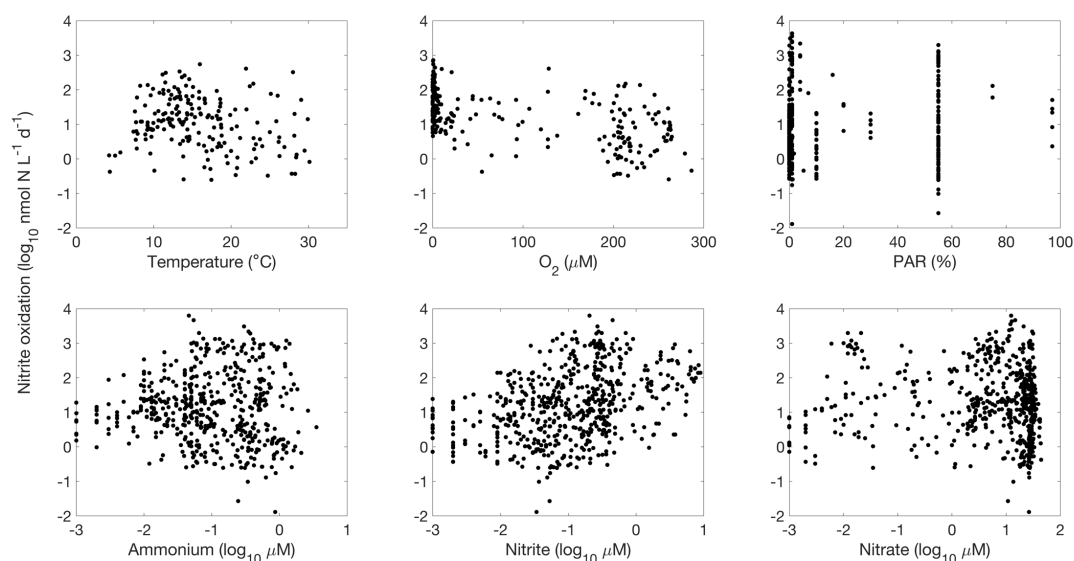
615 Figure 28. Relationship between ammonia oxidation rates and environmental factors.

616

617 Ammonia oxidation rates did not show a clear pattern with temperature ($r=-0.22$, $p<0.01$; Figure
618 28). Some of the high rates are found below 0°C , and at around 10°C and 25°C . Temperature
619 manipulation experiments showed varying temperature sensitivity of ammonia oxidation in
620 different regions or among natural assemblages (Baer et al., 2014; Horak et al., 2018; Zheng et al.,
621 2020). The highest ammonia oxidation rates were found in the oxygen range between 100 and 200
622 μM ($p>0.01$). But ammonia oxidation has also been detected in low oxygen waters (e.g., $<10 \mu\text{M}$)
623 in the oxygen minimum zones (Bristow et al., 2016a; Peng et al., 2015), reflecting the high affinity
624 of ammonia oxidizers for oxygen. Oxygen production by ammonia-oxidizing archaea may support
625 their presence and activity in the oxygen minimum zones (Kraft et al., 2022). Ammonia oxidation
626 generally decreases at relatively high light intensity (PAR% relative to surface PAR) due to light
627 inhibition and substrate competition with phytoplankton (but the negative slope is not significant,
628 $p > 0.01$). Nevertheless, high ammonia oxidation rates have been measured in the euphotic zone
629 at 55% PAR in the Atlantic Ocean (Clark et al., 2008; Clark et al., unpublished). Ammonia
630 oxidation increases with N nutrient concentration ($p<0.01$). NH_4^+ is the substrate while NO_2^- is the
631 product of ammonia oxidation. The Michaelis-Menten-like kinetics of ammonia oxidation rate
632 have been observed in various ocean regions (Frey et al., 2022; Newell et al., 2013; Horak et al.,
633 2013; Xu et al., 2019; Zhang et al., 2020; Mduyana et al., 2022a and b). High concentrations of



634 NH_4^+ and NO_2^- likely reflect intense recycling of organic matter and remineralization. The
635 presence of high NO_3^- concentration may relieve the competition between ammonia oxidizers and
636 phytoplankton for NH_4^+ , therefore leading to high ammonia oxidation rates (Wan et al., 2018). In
637 addition, recent studies have shown that AOA have a high requirement for iron and copper, which
638 may affect the distribution of nitrification in the ocean (Shafiee et al., 2019; Shafiee et al., 2021).
639

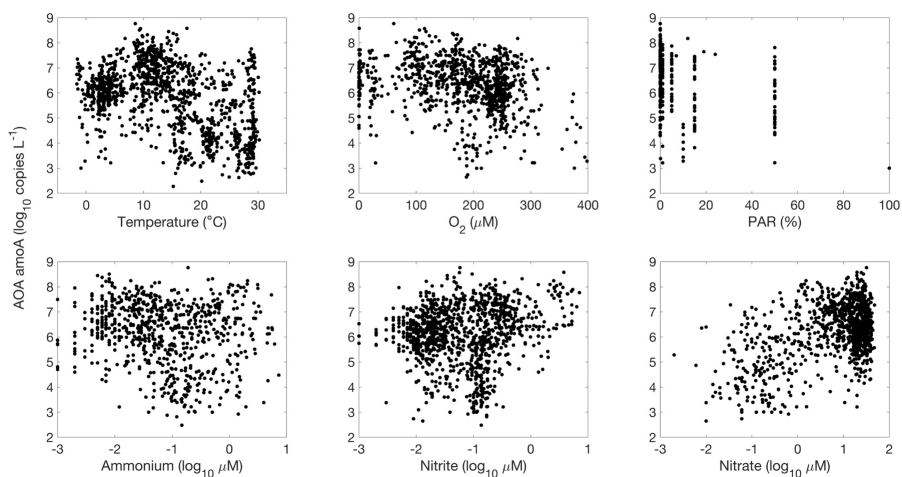


640
641 Figure 29. Relationships between nitrite oxidation rates and environmental factors.

642
643 High nitrite oxidation rates are found between 10°C and 20°C (Figure 28). Surprisingly, some of
644 the highest nitrite oxidation rates were measured in the oxygen minimum zones even with oxygen
645 levels below detection limits (Ward et al., 1989; Sun et al., 2017; Sun et al., 2021). Nitrite oxidation
646 in anoxic waters has been observed to be inhibited (Sun et al., 2017) or stimulated (Bristow et al.,
647 2016a) by the addition of oxygen. The mechanisms for apparently anaerobic nitrite oxidation
648 remain to be determined (Sun et al., 2023). Similar to ammonia oxidation, nitrite oxidation is often
649 reported to be inhibited by high light levels, but the relationship is not statistically significant
650 across the database ($p > 0.01$; Figure 29) partly due to the presence of high nitrite oxidation rates in
651 the euphotic zone (e.g., Clark et al., 2016). High nitrite oxidation rates are often observed in regions
652 with high NO_2^- concentration ($r = 0.23$, $p < 0.01$). For example, the highest nitrite oxidation rates
653 were observed at NO_2^- concentrations near 0.5 μM (Figure 29).



654



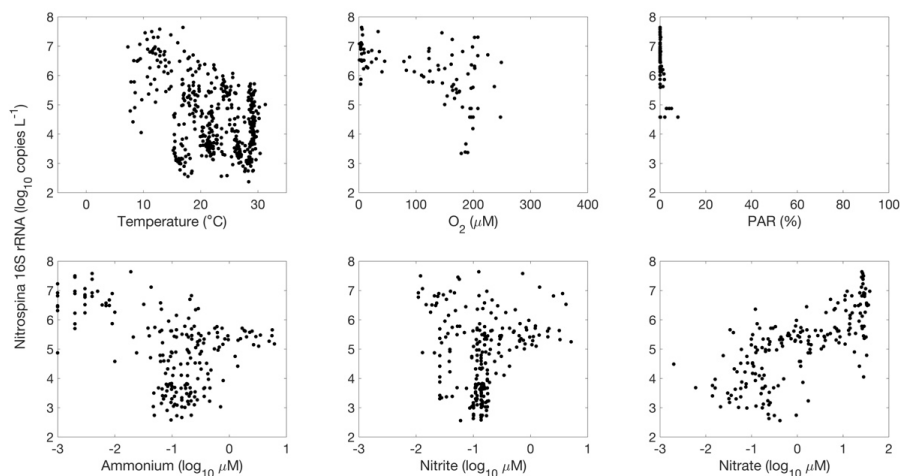
655

656 Figure 30. Relationship between archaeal *amoA* gene abundance and environmental factors.

657

658 We use *amoA* gene abundance to represent the abundance of ammonia oxidizers with the caveat
659 that the number of gene copies may not equal the cell numbers. Ammonia oxidizers are adapted to
660 a wide range of environmental conditions (Figure 30). Their abundance reaches a maximum at
661 around 10°C. Ammonia oxidizers are also present in low oxygen waters and the euphotic zone
662 with slightly lower abundance. Interestingly, ammonia oxidizers show relatively constant
663 abundance across the NH_4^+ concentration gradient while ammonia oxidation rates are low under
664 low NH_4^+ concentration (e.g., $<0.01 \mu\text{M}$).

665



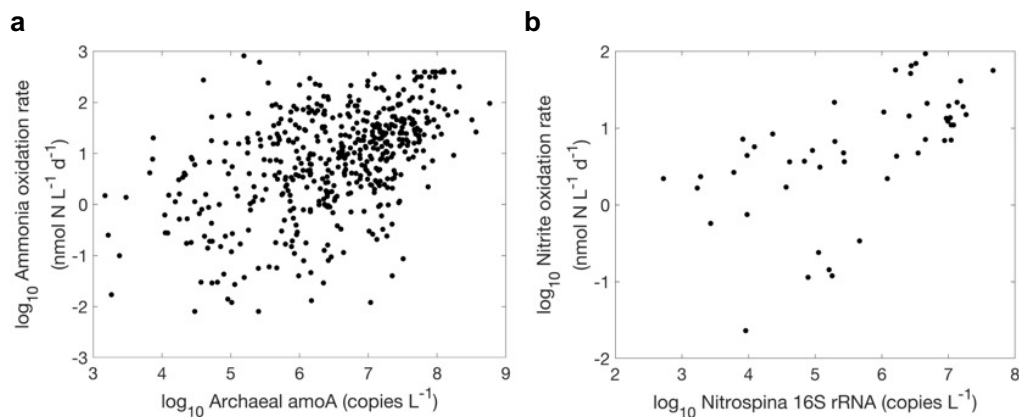
666

667 Figure 31. Relationships between *Nitrospina* 16S rRNA gene abundance and environmental
668 factors.

669

670 It is difficult to evaluate the relationship between nitrite oxidizers and environmental factors due
671 to the limited number of observations (Figure 31). Nevertheless, one interesting pattern is the
672 presence of high *Nitrospina* abundance in oxygen depleted waters. The nitrite oxidizers present in
673 the oxygen depleted waters are distinct from those found in oxygenated waters or currently
674 cultivated strains (Sun et al., 2019; Sun et al., 2021).

675



676



677 Figure 32. Relationships between nitrifier abundance and nitrification rate. (a) ammonia oxidation
678 vs AOA *amoA* gene abundance ($y=0.46*x-2.08$, $r=0.48$, $p<0.01$); (b) nitrite oxidation vs
679 *Nitrospina* 16S rRNA gene abundance ($y=0.35*x-1.27$, $r=0.59$, $p<0.01$).

680

681 There is a positive correlation between AOA *amoA* gene abundance and ammonia oxidation rates
682 ($r=0.44$, $p<0.01$), and between *Nitrospina* 16S rRNA abundance and nitrite oxidation rate ($r=0.58$,
683 $p<0.01$) (Figure 32) even though the correlation is weak. This lack of a strong relationship has also
684 been found in regional studies (Tolar et al., 2020), which may be caused by the perturbation of the
685 microbial community during rate measurement incubations. Furthermore, the addition of nitrogen
686 substrate during rate measurement incubations may stimulate the growth of nitrifiers and the
687 subsequently measured nitrification rate. Overall, using functional gene abundances to predict their
688 functional activity needs to be conducted with caution since the presence of genes only reflects the
689 functional potentials.

690

691 **Applications of the database and suggestions for future research**

692 This database will be useful for a broad scientific community who are interested in marine
693 biogeochemistry and marine microbial ecology. Potential applications include but are not limited
694 to: 1) Compare future measurements of nitrification rates or nitrifier abundance in a specific region
695 to previous measurements conducted in the same regions, and contextualize new measurements at
696 the global scale. 2) Meta-analysis of environmental controls on the distribution of nitrification and
697 nitrifier abundance at regional and global scales. The simple correlation analyses provided here
698 only considered individual environmental drivers separately while other drivers are changing
699 simultaneously. Analysis with environmental assemblages could complement laboratory culture
700 experiments. 3) Help to validate and improve model parametrization of nitrification and nitrifiers.
701 For example, ammonia oxidation has been modeled as a function of substrate concentration and
702 specific ammonia oxidation rate (Yool et al., 2007). However, nitrification has been found to be
703 regulated by temperature, oxygen, light and many other environmental factors that are not
704 considered in that model. A better representation of nitrification in ocean biogeochemical models
705 could help to constrain the estimates of marine new production, N₂O production and many other
706 key processes. 4) Guide future nitrification studies, e.g., conducting measurements in poorly
707 sampled regions or seasons.



708

709 Based on the historical measurements of nitrification and nitrifiers, we provide recommendations
710 for future research below.

711

712 1. Method standardization is useful for comparison among studies. Nitrification has been mostly
713 measured by ^{15}N substrate tracer addition and product dilution methods. The ^{15}N product dilution
714 method tends to yield higher rates relative to the ^{15}N substrate tracer addition method (Figure 1).
715 This is perhaps to be expected since the ^{15}N product dilution method measures all the NO_2^-
716 production pathways including ammonia oxidation (and organic N oxidation) and nitrate reduction
717 instead of only NO_2^- production from ammonia oxidation as is measured by the $^{15}\text{NH}_4^+$ tracer
718 addition method. Comparison between different methods should be conducted to resolve the
719 difference or even correct some of the previous measurements.

720

721 Additionally, the amount of tracer added should be recorded and reported because the increased
722 substrate concentration may enhance nitrification rate. Therefore, the measured rates should be
723 interpreted as potential rates rather than in-situ rates when the amount of tracer addition is large
724 compared to the ambient substrate concentration. If possible, substrate kinetic experiments should
725 be conducted for in-situ rate calibration (e.g., Wan et al., 2018; Mduyana et al., 2022a and b).

726

727 The measured product of ammonia oxidation should also be reported (e.g., either only NO_2^- or
728 $\text{NO}_2^- + \text{NO}_3^-$). When ambient NO_2^- concentration is low, the $^{15}\text{NO}_2^-$ produced from $^{15}\text{NH}_4^+$ tracer
729 may be further oxidized to $^{15}\text{NO}_3^-$. Thus, nitrification may be underestimated if only NO_2^- is
730 measured. Alternatively, NO_2^- carrier may be added into the incubation to ‘trap’ the produced
731 $^{15}\text{NO}_2^-$. In addition to only measuring ammonia oxidation, more observations of nitrite oxidation
732 are desirable to evaluate mechanisms controlling the coupling or decoupling of the two steps of
733 nitrification.

734

735 Furthermore, measurements with at least three time points are preferred during the incubation time
736 courses in order to examine whether the rate has changed during the incubation period. Depending
737 on the incubation period, nitrification rates are reported as either $\text{nmol N L}^{-1} \text{d}^{-1}$ or $\text{nmol N L}^{-1} \text{h}^{-1}$.
738 A conversion factor (e.g., 12 or 24 hours) is required to obtain the same unit. The choice of the



739 conversion factor may be critical if there is a diel cycle of nitrification rate, e.g., in the euphotic
740 zone where light/solar radiation varies diurnally (Wan et al., 2021). Therefore, incubation
741 conducted under both light and dark conditions may be preferable to obtain the daily nitrification
742 rates. The detection limit of rate measurements should also be estimated and reported (Santoro et
743 al., 2013) instead of presenting rates that are below detection limit as zero.

744

745 For in-situ rate measurements, incubations should mimic the in-situ environmental conditions as
746 closely as possible, e.g., using light filters to simulate in-situ light/solar radiation intensity and
747 quality; using a temperature-controlled incubator to simulate the in-situ temperature. Particularly
748 for samples collected in the oxygen minimum zones, oxygen concentration in the incubation
749 containers should be measured or monitored throughout the incubation because oxygen
750 contamination is common during the sampling process (Garcia-Robledo et al., 2021). Samples
751 collected from the anoxic layer of the oxygen minimum zones need to be purged with helium or
752 nitrogen gas to remove any oxygen contamination before incubation.

753

754 2. Various primers have been designed to target ammonia oxidizers. However, current primers
755 miss the *Nitrosopumilus*-like *amoA* (Tolar et al., 2013; Hiraoka et al., preprint) and such group
756 accounts for a large fraction of the AOA based on 16S rRNA sequencing (Tolar et al., 2020). New
757 primers or techniques need to be developed to cover the diverse groups of ammonia oxidizers. In
758 addition, the quantification of nitrite oxidizers is limited. Developing primers for *nxr* genes may
759 be useful to untangle the relative contribution of different nitrite oxidizers particularly for the
760 unique ones found in the oxygen minimum zones. The report of qPCR assay should follow the
761 MIQE guidelines (Bustin et al., 2009) including the amplification conditions, amplification
762 efficiency, detection limit and other parameters. Alternatively, the abundance of nitrifiers may be
763 determined with quantitative metagenomics (Lin et al., 2019; Satinsky et al., 2013). In comparison
764 to the gene presence, gene expression and protein synthesis may be better linked to the activity of
765 nitrifiers (Tolar et al., 2016; Frey et al., 2022; Saito et al., 2020), deserving more observations.

766

767 3. Future observations should target regions that have been poorly sampled and regions that are
768 experiencing or expected to experience dramatic changes. For example, the Indian Ocean has the
769 fewest number of observations of nitrification and nitrifiers. With regards to change, oxygen



770 minimum zones are projected to change under future climate (Breitburg et al., 2018; Busecke et
771 al., 2022). Polar oceans (Arctic Ocean and Southern Ocean) are experiencing warming, ice melt
772 (which affects light/solar radiation availability) and ocean acidification (Meredith et al., 2019).
773 Upward nutrient supply into the subtropical gyres may be affected due to enhanced stratification
774 (Li et al., 2020). How nitrification will respond to these changes deserves further exploration.

775

776 Time-series studies, observations across a large-scale transect, and observations at a mesoscale or
777 submesoscale would be desirable for investigating the temporal and spatial variation of
778 nitrification rates and nitrifier abundances. When possible, both nitrification rates and nitrifier
779 abundance should be measured at the same locations. While this approach incurs logistical and
780 financial complications in requiring collaborations among laboratories with different expertise, the
781 benefit to comprehensive process description is manifold.

782

783 4. Incubation conditions (mentioned in point 2) and ambient environmental conditions associated
784 with rate measurements or gene quantification should be recorded and reported (e.g., temperature,
785 light, substrate concentration, oxygen). This information would be helpful for comparison among
786 different studies and future meta-analyses of environmental controls on nitrification and nitrifiers.
787 For example, light/solar radiation should be reported as both absolute light/solar radiation intensity
788 and relative light/solar radiation intensity to the surface ocean. Analysis of trace metals like iron
789 and copper concentration will be useful to assess their impact on nitrification. Standard notation
790 should be used to denote measurements below detection limit or measurements not conducted,
791 e.g., BDL for below detection limit, NM for not measured, empty/NA for data not available. A
792 data compilation template is provided for anyone who is interested in contributing to the database
793 with new datasets or datasets currently not included in the database. We encourage the scientific
794 community to contact us with suggestions to improve the database and to contribute to the database
795 with new datasets or datasets currently not included in the database.

796

797 **Data availability**

798 Data described in this manuscript can be accessed at Zenodo repository under data doi:

799 <https://doi.org/10.5281/zenodo.7942922> (Tang et al., 2023).



800

801 **Conclusions**

802 We present a newly compiled database of nitrification rate and nitrifier abundance measurements
803 in the global ocean. This database sheds light on the spatial and temporal pattern of nitrification
804 and nitrifiers even though the spatial and temporal coverages remain limited. In recent years,
805 observations have expanded into oxygen minimum zones and polar oceans while the Indian Ocean
806 and Pacific Basin remain poorly sampled, especially with regard to nitrite oxidation and nitrite
807 oxidizers. This database can be applied to assess the environmental controls on nitrification at
808 regional and global scales, to validate and develop biogeochemical models, to guide future
809 observational efforts, and to better constrain the distribution of nitrification and assess its impact
810 on the marine ecosystem and climate. This database has been deposited into the Zenodo repository
811 and can be updated with new datasets.

812

813 **Author contributions**

814 Weiyi Tang and Bess Ward designed the study with input from Fabien Paulot and Charles Stock.
815 Weiyi Tang compiled the database with data contribution from coauthors, and Weiyi Tang
816 analyzed the database. Weiyi Tang and Bess Ward wrote the manuscript with contribution from
817 coauthors.

818

819 **Competing interests**

820 No competing interest is declared.

821

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