Database of nitrification and nitrifiers in the global ocean

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Abstract

As a key biogeochemical pathway in the marine nitrogen cycle, nitrification (ammonia oxidation and nitrite oxidation) converts the most reduced form of nitrogen – ammonium/ammonia (NH_4^+/ NH_3) into the oxidized species nitrite (NO_2^-) and nitrate (NO_3^-). In the ocean, these processes are mainly performed by ammonia-oxidizing archaea (AOA) and bacteria (AOB), and nitrite-oxidizing bacteria (NOB). By transforming nitrogen speciation and providing substrates for nitrogen removal, nitrification affects microbial community structure, marine productivity (including chemoautotrophic carbon fixation) and the production of a powerful greenhouse gas, nitrous oxide (N_2O). Nitrification is hypothesized to be regulated by temperature, oxygen, light, substrate concentration, substrate flux, pH, and other environmental factors. Although the number of field observations from various oceanic regions has increased considerably over the last few decades, a global synthesis is lacking, and understanding how environmental factors control nitrification remains elusive. Therefore, we have compiled a database of nitrification rates and nitrifier abundance in the global ocean from published literature and unpublished datasets. This database includes 2393 and 1006 measurements of ammonia oxidation and nitrite oxidation rates, and 2242 and 631 quantifications of ammonia oxidizers and nitrite oxidizers, respectively. This community effort confirms and enhances our understanding of the spatial distribution of nitrification and nitrifiers, and their corresponding drivers such as the important role of substrate concentration in controlling nitrification rates and nitrifier abundance. Some conundrums are also revealed including the inconsistent observations of light limitation and high rates of nitrite oxidation reported from anoxic waters. This database can be used to constrain the distribution of marine nitrification, to evaluate and improve biogeochemical models of nitrification, and to quantify the impact of nitrification on ecosystem functions like marine productivity and N_2O production. This database additionally sets a baseline for comparison with future observations and guides future exploration (e.g., measurements in the poorly sampled regions such as the Indian Ocean; method comparison/standardization). The database is publicly available at Zenodo repository: https://doi.org/10.5281/zenodo.8355912 (Tang et al., 2023).

Introduction

Nitrification (ammonia oxidation and nitrite oxidation) converts the most reduced form of nitrogen (N) – ammonium/ammonia (NH_4^+/NH_3) into the oxidized compounds nitrite (NO_2^-) and nitrate (NO_3^-). Ammonia oxidation is conducted by ammonia oxidizing archaea (AOA) and bacteria (AOB) with AOA dominating in most marine environments (Francis et al., 2005; Wuchter et al., 2006). Marine AOA are often separated into a few major ecotype groups including water column group A, water column group B and *Nitrosopumilus*-like (Beman et al., 2008; Tolar et al., 2020), with a diverse group of AOA remaining to be characterized (Alves et al., 2018). Marine nitrite oxidation is carried out by nitrite-oxidizing bacteria (NOB) such as *Nitrospina*, *Nitrospira*, *Nitrococcus* and *Nitrobacter*, with *Nitrospina* as the dominant group (Mincer et al., 2007; Pachiadaki et al., 2017). Complete ammonia-oxidizing (comammox) bacteria within the bacterial genus *Nitrospira* have been identified in freshwater, terrestrial, and coastal environments but not yet been found in the open ocean (Daims et al., 2015; Van Kessel et al., 2015; Xia et al., 2018).

Nitrification and nitrifiers are thought to be regulated by light/solar radiation, oxygen, temperature, substrate concentration, pH, and other environmental factors (Ward, 2008), many of which are experiencing dramatic changes in the ocean. For example, light is generally found to inhibit nitrifier growth and nitrification rate (Olson. 1981b; Merbt et al., 2012; Xu et al., 2019). In addition, ocean acidification decreases ammonia oxidation rates (Beman et al., 2011; Breider et al., 2019) partly due to the decreased availability at lower pH of NH_3, which is the actual substrate for ammonia oxidation (Suzuki et al., 1974). In contrast, ocean warming shifts the NH_4^+/NH_3 equilibrium towards NH_3 by decreasing the pK_a (Emerson et al., 1975) and is observed to enhance enzyme activity (Zheng et al., 2017; Zheng et al., 2020), further complicating the effect of climate change on nitrification.

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

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$0.13-1.4 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; Mdutyana 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

Methods

Data sources and compilation

Nitrification rates including ammonia oxidation and nitrite oxidation, and abundances of ammonia oxidizers and nitrite oxidizers were extracted directly from the literature published between 1984 and 2022 when the data were presented in tables or supplementary materials from publications; otherwise, data were provided by the coauthors. Some previously unpublished data were also included in the database. Table 1 and Table 2 summarize the origin, methods and locations of nitrification rate and nitrifier abundance measurements, sorted in alphabetical order by lead author. The metadata format contains geographical sampling information (date, latitude, longitude, and depth) and concurrent measurements of environmental conditions such as light intensity, temperature, salinity, water density, N concentration (NH_4^+, NO_2^- and NO_3^-), pH and oxygen concentration if available. In total, there are 2393, 1006, 2242, and 631 measurements of ammonia oxidation rate, nitrite oxidation rate, ammonia oxidizer abundance and nitrite oxidizer abundance, respectively. However, not all measurements of nitrification rates or nitrifier abundance are accompanied by all the environmental factors because such factors were often not reported in the literature or recorded during the measurements/sample collections. Rates, nitrifier abundances and environmental parameters below the methodological detection limits are noted as BDL. NM represents parameters that were not measured. Empty/NA means that data are not available or reported. The database is deposited into Zenodo repository following the Findable, Accessible, Interoperable and Reusable (FAIR) principles for data management (Wilkinson et al., 2016). We encourage authors and readers to contact us to report an update to or an error in the database.

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

References	Nitrification					Sampling regions	ammonia oxidizer?	nitrite oxidizer?
	Ammonia oxidation	Method	Analyte	Nitrite oxidation	Method			
Baer et al., 2017	6	$^{15}NH_4^+$ tracer addition	NO_2^- + NO_3^-			Western Coastal Arctic	No	No

Reference		Method 1	Species 1		Method 2	Location		
Beman et al., 2012	68	$^{15}NH_4^+$ tracer addition	NO_2^-+ NO_3^-	64	$^{15}NO_2^-$ tracer addition	Eastern Tropical North Pacific	Yes	No
Beman et al., 2021	78	$^{15}NH_4^+$ tracer addition	NO_2^-+ NO_3^-	79	$^{15}NO_2^-$ tracer addition	Eastern Tropical North Pacific	No	No
Bianchi et al., 1997	21	$H^{14}CO_3^-$ tracer addition	Particulate organic carbon	21	$H^{14}CO_3^-$ tracer addition	Southern Ocean	No	No
Breider et al., 2019	10	$^{15}NH_4^+$ tracer addition	NO_2^-+ NO_3^-			Western North Pacific	No	No
Bristow et al., 2015	9	$^{15}NH_4^+$ tracer addition	NO_2^-	9	$^{15}NO_2^-$ tracer addition	Gulf of Mexico	No	No
Cavagna et al., 2015				39	$^{15}NO_3^-$ tracer dilution	Southern Ocean	No	No
Clark et al., 2008	32	$^{15}NO_2^-$ tracer dilution	NO_2^-	32	$^{15}NO_3^-$ tracer dilution	Atlantic	No	No
Clark et al., 2011	13	$^{15}NO_2^-$ tracer dilution	NO_2^-	13	$^{15}NO_3^-$ tracer dilution	Eastern North Atlantic (offshore of the Iberian Peninsula)	No	No
Clark et al., 2014	10	$^{15}NO_2^-$ tracer dilution	NO_2^-	10	$^{15}NO_3^-$ tracer dilution	Northwest European shelf sea	No	No
Clark et al., 2016	21	$^{15}NO_2^-$ tracer dilution	NO_2^-	42	$^{15}NO_3^-$ tracer dilution	Mauritanian upwelling system	No	No
Clark et al., 2022	88	$^{15}NO_2^-$ tracer dilution	NO_2^-			Atlantic	No	No
Clark et al., unpublished 1	18	$^{15}NO_2^-$ tracer dilution	NO_2^-	18	$^{15}NO_3^-$ tracer dilution	Eastern North Atlantic	No	No
Clark et al., unpublished 2	18	$^{15}NO_2^-$ tracer dilution	NO_2^-	18	$^{15}NO_3^-$ tracer dilution	Eastern North Atlantic	No	No
Clark et al., unpublished 3	21	$^{15}NO_2^-$ tracer dilution	NO_2^-	21	$^{15}NO_3^-$ tracer dilution	Eastern North Atlantic	No	No
Clark et al., unpublished 4	11	$^{15}NO_2^-$ tracer dilution	NO_2^-	11	$^{15}NO_3^-$ tracer dilution	Subpolar North Atlantic and Arctic	No	No
Damashek et al., 2018	15	$^{15}NH_4^+$ tracer addition	NO_2^-+ NO_3^-			South Atlantic Bight	Yes	Yes
Diaz and Raimbault, 2000	20	$^{15}NH_4^+$ tracer addition	NO_2^-+ NO_3^-			Gulf of Lions in the Mediterranean Sea	No	No
Dore and Karl, 1996	11	NO_2^-+ NO_3^- concentration change over	NO_2^-+ NO_3^-, particulate	6	NO_3^- concentration	Station ALOHA in the North Pacific	No	No

Reference	n			n		Location		
		time; H^{14}CO$_3^-$ tracer addition	organic carbon			change over time		
Fernández et al., 2009	15	^{15}NH$_4^+$ tracer addition	NO$_2^-$+ NO$_3^-$			Peru upwelling system	No	No
Flynn et al., 2021				104	^{15}NO$_2^-$ tracer addition	Weddell Sea	No	No
Frey et al., 2020	21	^{15}NH$_4^+$ tracer addition	NO$_2^-$			Eastern Tropical South Pacific	Yes	No
Frey et al., 2022	30	^{15}NH$_4^+$ tracer addition	NO$_2^-$			Eastern Tropical North Pacific	Yes	No
Ganesh et al., 2015	5	^{15}NH$_4^+$ tracer addition	NO$_2^-$	5	^{15}NO$_2^-$ tracer addition	Eastern Tropical North Pacific oxygen minimum zone	No	No
Kalvelage et al., 2011	6	^{15}NH$_4^+$ tracer addition	NO$_2^-$			Namibian oxygen minimum zone	No	No
Kalvelage et al., 2013	108	^{15}NH$_4^+$ tracer addition	NO$_2^-$	110	^{15}NO$_2^-$ tracer addition	Eastern Tropical South Pacific oxygen minimum zone	Yes	No
Kitzinger et al., 2020	9	^{15}NH$_4^+$ tracer addition	NO$_2^-$	9	^{15}NO$_2^-$ tracer addition	Gulf of Mexico	No	No
Lam et al., 2009	14	^{15}NH$_4^+$ tracer addition	NO$_2^-$			Eastern Tropical South Pacific	No	No
Laperriere et al., 2020	59	^{15}NH$_4^+$ tracer addition	NO$_2^-$+ NO$_3^-$			Southern California Bight	No	No
Liu et al., 2018	86	^{15}NH$_4^+$ tracer addition	NO$_2^-$+ NO$_3^-$			South Atlantic Bight	Yes	Yes
Liu et al., 2022	10	^{15}NH$_4^+$ tracer addition	NO$_2^-$+ NO$_3^-$			South China Sea	No	No
Mccarthy et al., 1999	8	^{15}NH$_4^+$ tracer addition	NO$_2^-$+ NO$_3^-$			Arabian Sea	No	No
Mdutyana et al., 2020	59	^{15}NH$_4^+$ tracer addition	NO$_2^-$	38	^{15}NO$_2^-$ tracer addition	Southern Ocean	No	No
Mdutyana et al., 2022a	24	^{15}NH$_4^+$ tracer addition	NO$_2^-$			Southern Ocean	No	No
Mdutyana et al., 2022b				24	^{15}NO$_2^-$ tracer addition	Southern Ocean	No	No
Newell et al., 2013	8	^{15}NH$_4^+$ tracer addition	NO$_2^-$			Sargasso Sea (western North Pacific)	No	No
Peng et al., 2015	30	^{15}NH$_4^+$ tracer addition	NO$_2^-$, NO$_2^-$ + NO$_3^-$	30	^{15}NO$_2^-$ tracer addition	Eastern Tropical North Pacific	Yes	No
Peng et al., 2016	47	^{15}NH$_4^+$ tracer addition	NO$_2^-$	47	^{15}NO$_2^-$ tracer addition	Eastern Tropical South Pacific	Yes	No

Reference	n	Method	Product	n	Method	Location		
Peng et al., 2018	28	$^{15}NH_4^+$ tracer addition	NO_2^-	28	$^{15}NO_2^-$ tracer addition	Subarctic North Atlantic	Yes	No
Raes et al., 2020	39	$^{15}NH_4^+$ tracer addition	$NO_2^- + NO_3^-$			South Pacific	No	No
Raimbault et al., 1999	41	$^{15}NH_4^+$ tracer addition	$NO_2^- + NO_3^-$			Equatorial Pacific	No	No
Santoro et al., 2010	11	$^{15}NH_4^+$ tracer addition	$NO_2^- + NO_3^-$			Central California Current	Yes	Yes
Santoro et al., 2013	10	$^{15}NH_4^+$ tracer addition	NO_2^-, $NO_2^- + NO_3^-$			Central California Current	Yes	No
Santoro et al., 2017	12	$^{15}NH_4^+$ tracer addition	$NO_2^- + NO_3^-$			Equatorial Pacific	Yes	No
Santoro et al., 2021	57	$^{15}NH_4^+$ tracer addition	$NO_2^- + NO_3^-$	57	$^{15}NO_2^-$ tracer addition	Eastern Tropical South Pacific	Yes	Yes
Sinyanya et al., unpublished				31	$^{15}NO_2^-$ tracer addition	Southwest Indian Ocean	No	No
Shiozaki et al., 2016	87	$^{15}NH_4^+$ tracer addition	$NO_2^- + NO_3^-$			Equatorial Pacific to the Arctic Ocean	Yes	No
Shiozaki et al., 2019	56	$^{15}NH_4^+$ tracer addition	$NO_2^- + NO_3^-$			Arctic Ocean	Yes	No
Shiozaki et al., 2021	28	$^{15}NH_4^+$ tracer addition	$NO_2^- + NO_3^-$			Arctic Ocean	Yes	No
Smith et al., 2022	11	$^{15}NH_4^+$ tracer addition	NO_2^-			Southern Ocean	No	No
Sun et al., 2017				9	$^{15}NO_2^-$ tracer addition	Eastern Tropical North Pacific	No	No
Sutka et al., 2004	20	$^{15}NH_4^+$ tracer addition	$NO_2^- + NO_3^-$			North Pacific Subtropical Gyre to Eastern Tropical North Pacific	No	No
Tolar et al., 2016	73	$^{15}NH_4^+$ tracer addition	$NO_2^- + NO_3^-$			Antarctic coast	Yes	No
Tolar et al., 2017	38	$^{15}NH_4^+$ tracer addition	$NO_2^- + NO_3^-$			Georgia coast, South Atlantic Bight, Gulf of Alaska, Antarctic coast	Yes	No
Tolar et al., 2020	297	$^{15}NH_4^+$ tracer addition	$NO_2^- + NO_3^-$			Monterey Bay	Yes	No
Wallschuss et al., 2022	40	$^{15}NH_4^+$ tracer addition	NO_2^-	40	$^{15}NO_2^-$ tracer addition	Southeastern Atlantic	No	No

Wan et al., 2018	90	$^{15}NH_4^+$ tracer addition	$NO_2^-+NO_3^-$			South China Sea and Northwest Pacific	No	No
Wan et al., 2021	17	$^{15}NH_4^+$ tracer addition	NO_2^-	17	$^{15}NO_2^-$ tracer addition	North Pacific	No	No
Wan et al., 2022	85	$^{15}NH_4^+$ tracer addition	NO_2^-			North Pacific	No	No
Ward et al., 1984	16	$^{15}NH_4^+$ tracer addition	NO_2^-			Coastal waters off Washington	No	No
Ward, 1987	24	$^{15}NH_4^+$ tracer addition	NO_2^-		$^{15}NO_2^-$ tracer addition	Southern California Bight	No	No
Ward and Zafiriou, 1988	42	$^{15}NH_4^+$ tracer addition	NO_2^-			Eastern Tropical North Pacific	No	No
Ward et al., 1989	47	$^{15}NH_4^+$ tracer addition	NO_2^-	47	$^{15}NO_2^-$ tracer addition	Eastern Tropical South Pacific	No	No
Ward, 2005	110	$^{15}NH_4^+$ tracer addition	NO_2^-			Monterey Bay	No	No
Xu et al., 2018	78	$^{15}NH_4^+$ tracer addition	NO_2^-			South China Sea	No	No
Zhang et al., 2020	27	$^{15}NH_4^+$ tracer addition	NO_2^-	27	$^{15}NO_2^-$ tracer addition	South China Sea and Western Pacific	Yes	Yes
Total number of observations	2393			1006				

147

148 Table 2. Summary of the number of observations for nitrifier abundance from qPCR assays in
149 alphabetical order of the lead authors. The top row indicates the gene quantified for each group
150 (see text for further details). Whether nitrification rate is measured is indicated with yes or no. The
151 primers used for individual studies are identified in the database. AOA: ammonia-oxidizing
152 archaea; AOB: ammonia-oxidizing bacteria; NOB: nitrite-oxidizing bacteria.

References	*amoA*-based			*16S rRNA*-based			Sampling regions	ammonia oxidation	nitrite oxidation
	AOA	AOB	NOB	*Thaumarchaeota*	*Nitrospira*	*Nitrospina*			
Agogue et al., 2008	55	55		55			North Atlantic	No	No
Beman et al., 2012	64	64		64			Eastern Tropical North Pacific	Yes	Yes
Beman et al., 2013						63	Eastern Tropical North Pacific	Yes	Yes

Bristow et al., 2016b	27		27		Bay of Bengal oxygen minimum zone	No	No
Damashek et al., 2018.	34		34	34	South Atlantic Bight	Yes	No
Frey et al., 2020	21				South Pacific oxygen minimum zone	Yes	No
Frey et al., 2022	30				North Pacific oxygen minimum zone	Yes	No
Horak et al., 2018	6	6			North Pacific Ocean	Yes	No
Kalvelage et al., 2013	143	89			South Pacific oxygen minimum zone	Yes	Yes
Liu et al., 2018.	385	385	385	385	South Atlantic Bight	Yes	No
Peng et al., 2013	23				Arabian Sea and Eastern Tropical South Pacific	No	No
Peng et a., 2015	19	19			Eastern Tropical South Pacific	Yes	Yes
Peng et a., 2016	19	19			Subarctic North Atlantic	Yes	Yes
Santoro et al., 2010	17	17	17	17	Central California Current	Yes	No
Santoro et al., 2013	10	10			Central California Current	Yes	No
Santoro et al., 2017	148				Equatorial Pacific	Yes	No
Santoro et al., 2021	78	24	78	78	Eastern Tropical South Pacific	Yes	Yes
Shiozaki et al., 2016	87	87			North Pacific	Yes	No
Shiozaki et al., 2019	56	56			Arctic Ocean	Yes	No
Shiozaki et al., 2021	28	28			Arctic Ocean	Yes	No

Reference							Location		
Sintes et al., 2013	115			115			Tropical Atlantic and coastal Arctic	No	No
Sintes et al., 2016	364			364			Atlantic Ocean	No	No
Tolar et al., 2016	73	73					Antarctic coast	Yes	No
Tolar et al., 2017	38			38			Georgia coast, South Atlantic Bight, Gulf of Alaska, Antarctic coast	Yes	No
Tolar et al., 2020	297						Monterey Bay	Yes	No
Wuchter et al., 2006	20	20		20			Atlantic Ocean	No	No
Zakem et al., 2018	31						North Pacific	Yes	No
Zhang et al., 2020	54	54		54	54	54	South China Sea and Western Pacific	Yes	Yes
Total points	2242	1006	27	1224	54	631			

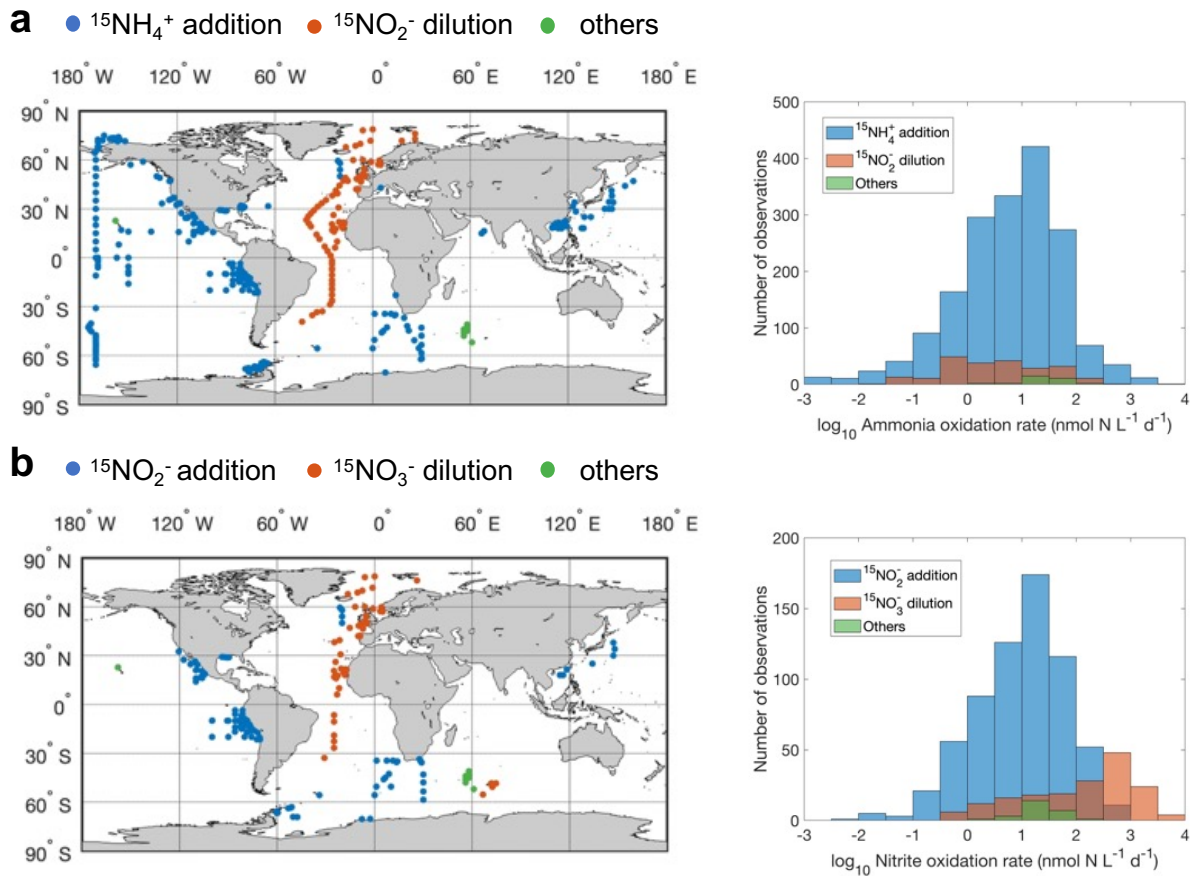
We applied Chauvenet's criterion for quality control to flag outliers in nitrification rates and nitrifier abundance (Glover et al., 2011). Chauvenet's criterion is commonly applied to normally distributed datasets to identify outliers whose deviations from the mean have a probability of less than $1/(2n)$, where n is the number of data points (Buitenhuis et al., 2013). We applied the criterion acknowledging the fact that the data were collected at different environmental conditions. After removing measurements of zero and below detection limit (277, 132, 51, 240, 6 and 11 observations for ammonia oxidation, nitrite oxidation, AOA *amoA*, AOB *amoA*, 16S rRNA of *Thaumarchaeota* and *Nitrospina*), nitrification rates and nitrifier abundances were log10 transformed before further analysis. Nitrification rates and nitrifier abundances reported at 0 or below detection limit are noted separately in the database and following analysis. Although we did not find outliers for ammonia oxidation and nitrite oxidation rates, there are some extreme values worth noting. For example, an extremely high ammonia oxidation rate of 4900 nmol L^{-1} d^{-1} was observed in the Peruvian oxygen minimum zone (Lam et al., 2009). Low but detectable rates below 0.01 nmol L^{-1} d^{-1} were observed in the Eastern Tropical North Pacific oxygen minimum zone (Frey et al., 2022), South Atlantic Bight (Liu et al., 2018) and western Pacific (Xu et al., 2018). Some

169 outliers were identified by Chauvenet's criterion for ammonia oxidizers (1 for AOB *amoA* and 1
170 for 16S rRNA of *Thaumarchaeota*). An abnormally high abundance of the bacterial *amoA* gene
171 (10^8 copies L^{-1}) was observed in the South Pacific oxygen minimum zone (Kalvelage et al., 2013),
172 which was removed from the following analysis. A low abundance of 16S rRNA of
173 *Thaumarchaeota* (25 copies L^{-1}) was found in the surface water of the western Pacific (Zhang et
174 al., 2020). In addition, the low-ammonia concentration AOA ecotype (or water column group B
175 AOA) at 2 copies L^{-1} was reported in the Arctic Ocean (Sintes et al., 2013). Measurements of
176 nitrification rate and nitrifier abundance of 0 or below detection limit were not included in the
177 analysis of outlier identification. For example, AOA abundance at 0 or below detection limit
178 (varies among studies) has been reported in surface waters of South Atlantic Bight (Damashek et
179 al., 2018), equatorial Pacific (Santoro et al., 2017) and North Pacific (Shiozaki et al., 2016).
180

181 **Methods for measuring ammonia oxidation and nitrite oxidation rates**
182 Ammonia oxidation rate is commonly measured by comparing the change in nitrite (NO_2^-) and
183 nitrate (NO_3^-) concentration in controls versus an experimental treatment containing a nitrification
184 inhibitor (e.g., Dore and Karl, 1996), by tracking the oxidation of $^{15}NH_4^+$ into the NO_2^- and NO_3^-
185 pool (Olson, 1981a), or by the dilution of $^{15}NO_2^-$ (Clark et al., 2007). Similarly, nitrite oxidation
186 rate can be measured by the change in NO_3^- concentration, by tracking the oxidation of $^{15}NO_2^-$ into
187 the NO_3^- pool, or by the dilution of $^{15}NO_3^-$ (Ward et al., 1989). In addition, nitrification has also
188 been estimated from the incorporation of ^{14}C tracer due to the chemoautotrophic metabolism of
189 nitrifiers (Bianchi et al., 1997). There is a large uncertainty, however, in the conversion factor from
190 carbon fixation to nitrification (Bayer et al., 2022). A more detailed description of methods for
191 measuring nitrification can be found in Ward, 2011a. The spatial distribution of different methods
192 used to measure nitrification and the frequency distribution of measured rates by different methods
193 are shown in Figure 1. Rates measured with the substrate tracer addition method ($^{15}NH_4^+$ and
194 $^{15}NO_2^-$) outnumbered other methods globally but the product dilution method ($^{15}NO_2^-$ and $^{15}NO_3^-$)
195 dominated in the Atlantic Ocean. The ammonia oxidation rates measured by different methods
196 have similar median values. However, the median nitrite oxidation rate measured by the $^{15}NO_3^-$
197 dilution method is significantly higher than the rate measured by the $^{15}NO_2^-$ addition method (200.3
198 vs 7.4 nmol N L^{-1} d^{-1}). These comparisons, however, are between samples aggregated from
199 measurements taken at different sites. It is thus unclear whether the differences arise from

200 differences in the measurement approaches (e.g., in sensitivity) or in the sites where measurements

201 were made. A direct methods comparison is recommended for future exploration.

202

203

204 Figure 1. Distribution of different methods used to measure ammonia oxidation (a) and nitrite

205 oxidation (b). Others include ^{14}C incorporation and concentration change methods. Note the colors

206 change slightly where they overlap in the histograms.

207

208 Incubations to measure nitrification rates have been conducted in polycarbonate and glass bottles,

209 exetainers and plastic bags. Seawater is directly transferred from the Niskin bottle into the

210 incubation containers to minimize temperature, oxygen and other perturbations. These incubation

211 containers are usually kept in an incubator with light filters to mimic the ambient temperature and

212 light conditions. After incubating for 3 hours to over 24 hours depending on the estimated

213 magnitude of nitrification rates, the incubation is terminated by filtering via GF/F or 0.22 µm filters

214 (e.g., Baer et al., 2017; Wan et al., 2018). The filtrate is then frozen at -20ºC or -80ºC until further

215 analysis on land. The incubation has also been terminated by subsampling and freezing without

216   filtration (e.g., Damashek et al., 2018). Alternatively, the incubation is preserved by adding

217   mercury chloride or zinc chloride (Kalvelage et al., 2013; Frey et al., 2020). This method allows

218   gas measurements like N_2O and N_2 production before nitrification analysis. Detailed incubation

219   conditions for each study are presented in the database file.

220

221   Various approaches have been developed to measure the N isotopes of NO_2^- and NO_3^-. For

222   example, 1) dissolved NO_2^- is extracted by formation of an azo dye. The resulting dye is filtered

223   onto precombusted GF/F or GF/C filters and its $^{15}N{:}^{14}N$ ratio is analyzed by elemental analyzer

224   isotope ratio mass spectrometry (Ward et al., 1982; Olson, 1981a). NO_3^- can be reduced to NO_2^-

225   by cadmium reduction and then extracted using the azo dye method described above. 2) Dissolved

226   NO_2^- is converted to Sudan-1 and Sudan-1 is collected via solid-phase extraction. The sample is

227   then purified by HPLC and derivatized before analysis by GC/MS (Clark et al., 2007). Similarly,

228   NO_3^- can be reduced to NO_2^- by cadmium prior to conversion to Sudan-1 for nitrogen isotope

229   analysis. 3) NO_2^- can be converted to N_2 with sulfamic acid and subsequently measured by isotope

230   ratio mass spectrometry (Dalsgaard et al., 2012; Bristow et al., 2016). 4) NO_2^- can also be

231   converted into N_2O by the azide method and subsequently measured by isotope ratio mass

232   spectrometry (Mcilvin and Altabet, 2005). The N isotopes of NO_2^- and NO_3^- can be measured via

233   the denitrifier method (Sigman et al., 2001; Weigand et al., 2016) where both NO_2^- and NO_3^- are

234   converted into N_2O. In addition, the $\delta^{15}N$ of NO_3^- alone can be measured using the denitrifier

235   method after removing NO_2^- with sulfamic acid (Granger and Sigman, 2009). The azide and

236   denitrifier methods require smaller sample volumes and offer a higher sensitivity of nitrogen

237   isotope detection.

238

239   Many factors may complicate the interpretation of rate measurements, e.g., isotope dilution by

240   regeneration of the ^{15}N-labeled substrates and stimulation of nitrification by substrate addition

241   (Lipschultz, 2008). For instance, the amount of tracer addition varied substantially from <10 nM

242   to 5 µM, enriching the ambient pool by <10% to over 1000%. The excess addition of substrates

243   will likely enhance the nitrification rate, which will then reflect a potential rate instead of an in-

244   situ rate. In addition, the measurement of NO_2^- compared to $NO_2^- + NO_3^-$ could also lead to

245   variations in the estimates of the ammonia oxidation rates. Specifically, $^{15}NO_2^-$ produced from

246    $^{15}NH_4^+$ may be further oxidized to $^{15}NO_3^-$, especially when samples are low in NO_2^- concentration.

247   Ammonia oxidation rate may be underestimated if only $^{15}NO_2^-$ is measured instead of measuring

248   both $^{15}NO_2^-$ and $^{15}NO_3^-$ (Santoro et al., 2013; Peng et al., 2015). Therefore, NO_2^- carrier (to increase

249   the NO_2^- pool and trap the produced $^{15}NO_2^-$) may be added to the sample before incubation or both

250   NO_2^- and NO_3^- should be measured after incubation when ambient NO_2^- concentration is low. The

251     $^{15}NO_2^-$ isotope dilution method may overestimate ammonia oxidation rates because NO_2^- could

252   also be released from phytoplankton after assimilative nitrate reduction (Lomas and Lipschultz,

253   2006). These confounding factors may be difficult to quantify but worth recording and reporting

254   in publications for the sake of comparison among studies. In addition, a variety of approaches have

255   been applied to calculate nitrification rates. The following equations are commonly used to

256   estimate nitrification measured by the tracer addition (Equation 1; e.g., Peng et al., 2015) or tracer

257   dilution method (Equation 2; e.g., Clark et al., 2007; Cavagna et al., 2015). However, these

258   equations do not account for the effect of other processes such as the isotope dilution on rate

259   estimates. Please refer to other studies for the detailed rate correction processes (e.g., Lipschultz

260   et al., 1986; Santoro et al., 2010; Kanda et al., 1987).

261 $$Rate = \frac{\Delta[^{15}NO_x^-]}{F \times \Delta t} \quad \text{Equation 1}$$

262   where $\Delta[^{15}NO_x^-]$ represents the change in concentration of $^{15}NO_2^-$ or $^{15}NO_3^-$ between the end

263   and start of the incubation. F represents the fraction of ^{15}N such as ($\frac{^{15}NH_4^+}{^{15}NH_4^+ + ^{14}NH_4^+}$ or $\frac{^{15}NO_2^-}{^{15}NO_2^- + ^{14}NO_2^-}$)

264   in the initial substrate pool (NH_4^+ or NO_2^-). Δt is the length of incubation time.

265 $$Rate = \frac{\ln(\frac{R_t}{R_0})}{\ln(\frac{[NO_x^-]_t}{[NO_x^-]_0})} \times (\frac{\frac{[NO_x^-]_0}{[NO_x^-]_t}}{\Delta t}) \quad \text{Equation 2}$$

266   where R_t and R_0 represent ratios of $^{15}NO_x^-$ to $^{14}NO_x^-$ after and before the incubation, respectively.

267   NO_x^- is either NO_2^- or NO_3^-, which are used for calculating ammonia oxidation and nitrite

268   oxidation rates, respectively. $[NO_x^-]_t$ and $[NO_x^-]_0$ are NO_x^- concentration after and before the

269   incubation, respectively. Δt is the length of incubation time.

270

271   Nitrification supported by organic N substrates like urea and cyanate has been observed in the Gulf

272   of Mexico (Kitzinger et al., 2018), Pacific (Santoro et al., 2017; Wan et al., 2021), off the east

273   coast of the United States (Laperriere et al., 2020; Tolar et al., 2017), and in the polar oceans

274   (Alonso-Saez et al., 2012; Shiozaki et al., 2021). The number of these observations remains limited

275   compared to ammonia oxidation. They can be included in future editions of the database (i.e., not

276   included in the current database) and their role in the marine N cycle deserves future investigations.

Methods for quantifying ammonia oxidizers and nitrite oxidizers

We summarize the primers used to quantify nitrifier abundance based on both functional genes and 16S rRNA genes using quantitative PCR (qPCR) (Table 3). The cell abundance and biomass can be subsequently estimated based on the gene abundance, number of genes per cell and specific cell biomass (e.g., Kitzinger et al., 2020; Khachikyan et al., 2019). The oxidation of ammonia to hydroxylamine is catalyzed by ammonia monooxygenase, which is a multisubunit enzyme partially encoded by the *amoA* gene. Primers have been designed to quantify both bacterial and archaeal *amoA* genes (Rotthauwe et al., 1997; Francis et al., 2005; Hornek et al., 2006; Wuchter et al., 2006; Beman et al., 2008; Mosier and Francis, 2011; Sintes et al., 2013). Archaeal ammonia oxidizers are also separated into different ecotypes including Water Column ecotypes A and B (WCA and WCB), which preferentially inhabit the surface vs deep ocean, respectively, or high-ammonia concentration vs low-ammonia concentration groups, which dominate in high ammonia vs low ammonia concentration environments, respectively. The *nxrB* gene, which encodes the beta subunit of nitrite oxidoreductase for nitrite oxidation, has been used to quantify *Nitrospira* (Pester et al., 2014). However, no primers targeting *nxr* genes are available for other groups of nitrite oxidizers such as *Nitrospina*, which is the dominant group of nitrite oxidizers in the ocean (Beman et al., 2013; Pachiadaki et al., 2017). Primers have also been designed to quantify the 16S rRNA gene abundance of *Thaumarchaeota*, *Nitrospira*, and *Nitrospina* (Mincer et al., 2007; Graham et al., 2007). The abundance of nitrifiers can be useful for inferring and interpreting nitrification rates. In addition to qPCR, amplicon sequencing and quantitative metagenomics are also useful to determine the abundance of nitrifiers (Tolar et al., 2020; Lin et al., 2019; Satinsky et al., 2013) but these analyses are not included in the database.

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

Target	Name	Primer sequences (5'-3')	References
Gamma-bacterial *amoA*	amoA-1F	GGGGTTTCTACTGGTGGT	Rotthauwe et al., 1997
	amoA-2R or	CCCCTCKGSAAAGCCTTCTTC	
	amoA-r NEW	CCCCTCBGSAAAVCCTTCTTC	Hornek et al., 2006

Water Column ecotype A (WCA) archaeal-*amoA*	Arch-amoAFA Arch-amoAR	ACACCAGTTTGGYTACCWTCDGC GCGGCCATCCATCTGTATGT	Beman et al., 2008; Francis et al., 2005
Water Column ecotype B (WCB) archaeal-*amoA*	Arch-amoAFB Arch-amoAR	CATCCRATGTGGATTCCATCDTG GCGGCCATCCATCTGTATGT	Beman et al., 2008; Francis et al., 2005
Total archaeal-*amoA*	Arch-amoAF Arch-amoAR	STAATGGTCTGGCTTAGACG GCGGCCATCCATCTGTATGT	Francis et al., 2005
High-ammonia concentration archaeal-*amoA*	Arch-amoA-for Arch-amoA-rev	CTGAYTGGGCYTGGACATC TTCTTCTTTGTTGCCCAGTA	Wuchter et al., 2006
Low-ammonia concentration archaeal-*amoA*	Arch-amoA-for Arch-amoA-rev-New	CTGAYTGGGCYTGGACATC TTCTTCTTCGTCGCCCAATA	Wuchter et al., 2006 Sintes et al., 2013
Thaumarchaeota 16S rRNA	GI_751F GI_956R	GTCTACCAGAACAYGTTC HGGCGTTGACTCCAATTG	Mincer et al., 2007
nxr	nxrB169F nxrB638R	TACATGTGGTGGAACA CGGTTCTGGTCRATCA	Pester et al., 2014
Nitrospira 16S rRNA	Nspra-675f Nspra-746r	GCGGTGAAATGCGTAGAKATCG TCAGCGTCAGRWAYGTTCCAGAG	Graham et al., 2007
Nitrospina 16S rRNA	NitSSU_130F NitSSU_282R	GGGTGAGTAACACGTGAATAA TCAGGCCGGCTAAMCA	Mincer et al., 2007

302

Results and Discussion

Summary of the database

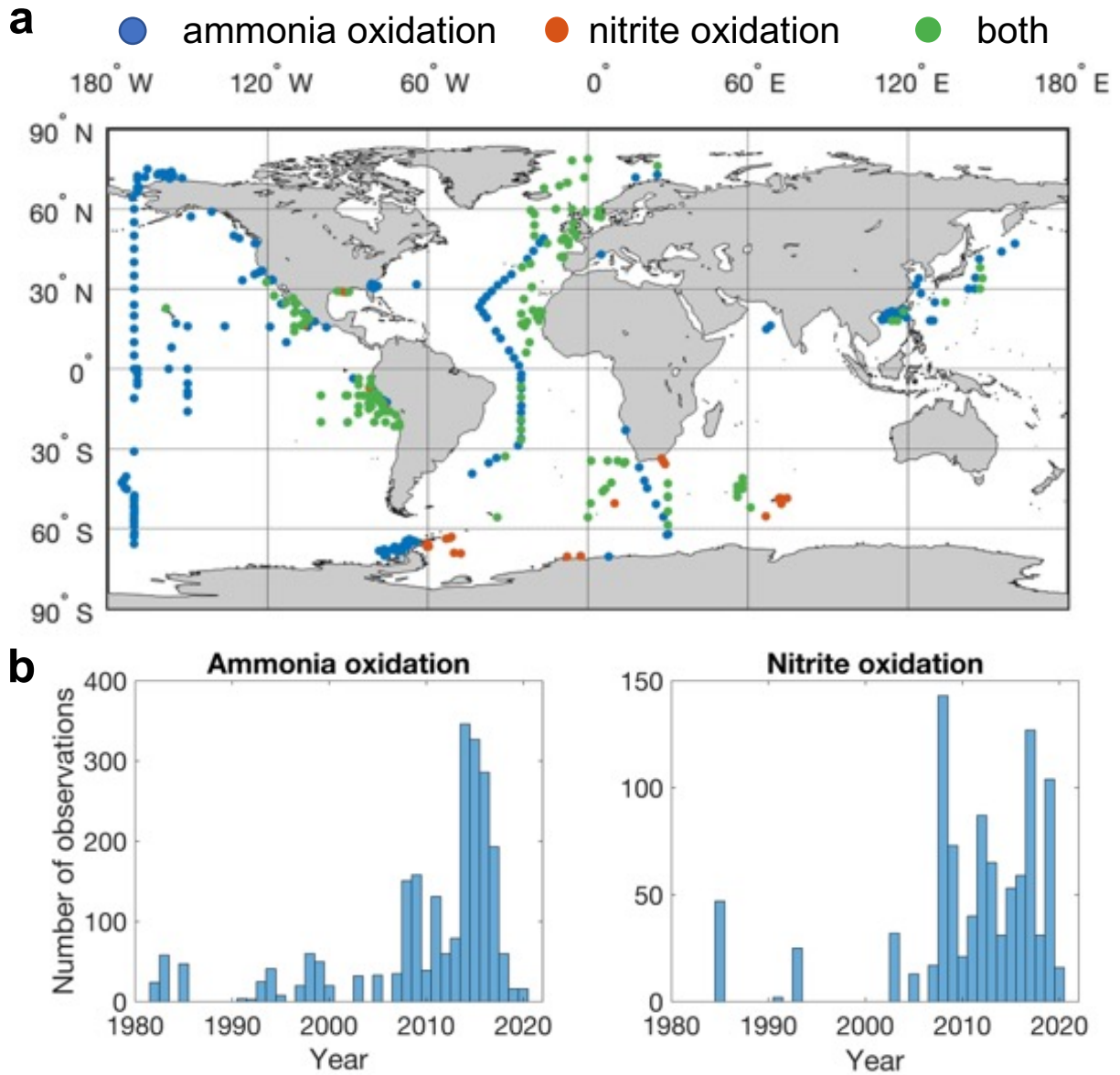



Figure 2. Map showing the distribution of sampling locations for nitrification rate measurements (a) and the number of observations each year (b). Blue points: only ammonia oxidation is measured; red points: only nitrite oxidation is measured. Green points: both ammonia oxidation and nitrite oxidation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

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

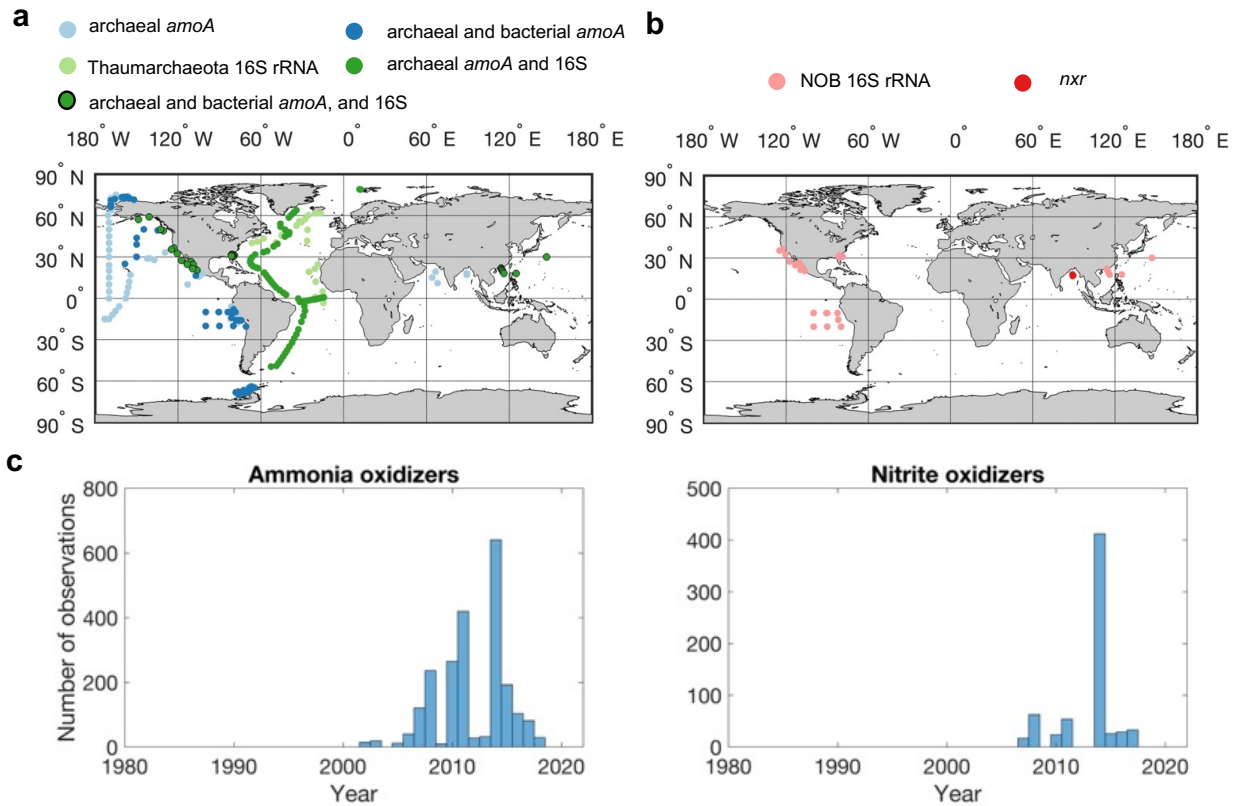



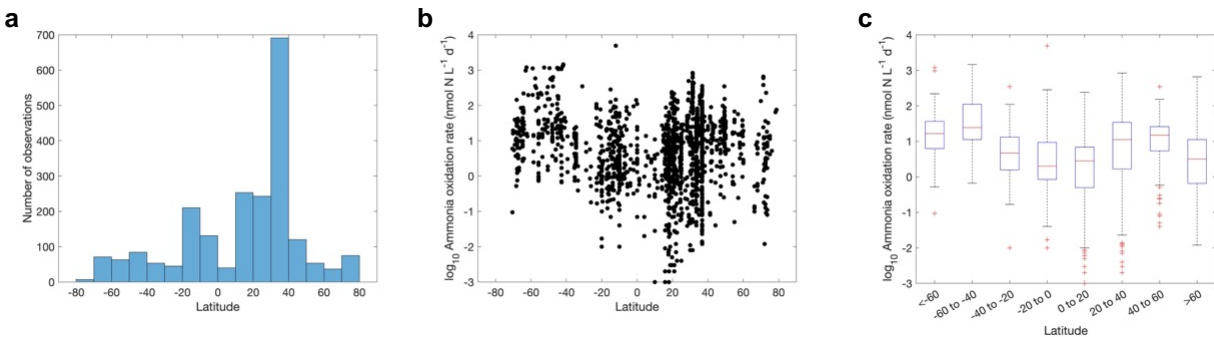
Figure 3. Maps showing the distribution of sampling locations for ammonia oxidizers (a) and nitrite oxidizers (b), and the number of observations each year (c). (a) light blue points: only archaeal *amoA* was quantified. Dark blue points: both archaeal and bacterial *amoA* genes were quantified. Light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

328 points: 16S rRNA of nitrite oxidizers was quantified; red points: *nxr* gene of nitrite oxidizers was
329 quantified.

330

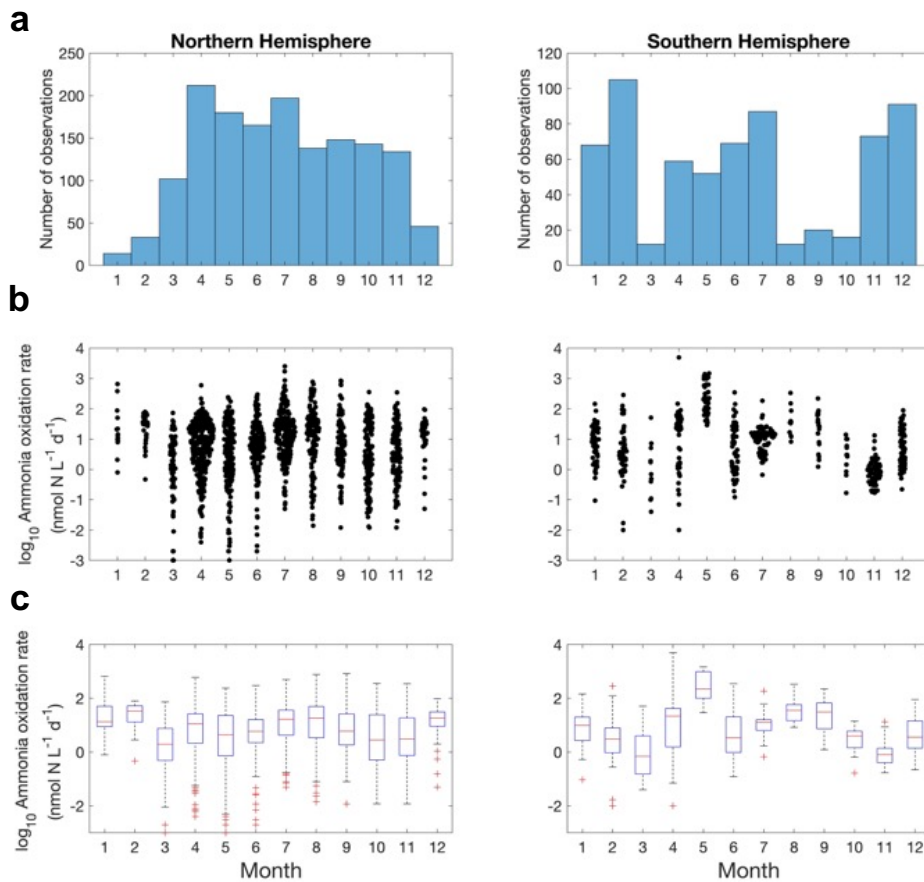
331 In total, there are 2242 and 631 measurements of ammonia oxidizer and nitrite oxidizer abundance,
332 respectively (Figure 3). Most of the nitrifier quantifications have been conducted in the tropical
333 and subtropical oceans (Figure 4a). Data are sparse in the central Pacific, Indian Ocean and
334 Southern Ocean (with the exception of the West Antarctic Peninsula). Both archaeal *amoA* and
335 16S rRNA genes of *Thaumarchaeota* were quantified on a transect across the Atlantic (Sintes et
336 al., 2016). There are far fewer observations of nitrite oxidizers compared to ammonia oxidizers.
337 Notably, there are only 27 observations of *nxr* genes. The quantification of nitrifier abundance
338 starts to accumulate after 2002 (Figure 3c). Most of the observations of nitrite oxidizers originate
339 from one study where samples were collected in 2014 (Liu et al., 2018). Nitrification rate and
340 nitrifier abundance are sometimes determined at the same location, which allows us to assess the
341 relationship between biogeochemical rate and the abundance of functional groups (e.g., Peng et
342 al., 2015; Shiozaki et al., 2019; Santoro et al., 2021).

343

344 **Distribution of ammonia oxidation**

345
346 Figure 4. Number of ammonia oxidation observations (a) and ammonia oxidation rates (b-c) within
347 latitudinal bands. For the boxplot in this figure and figures throughout the manuscript, the red line
348 in each box is the median. The bottom and top of each box are the 25th and 75th percentiles of the
349 observations, respectively. The error bars represent 1.5 times the interquartile range away from the
350 bottom or top of the box, with red + signs showing outliers beyond that range.

351

352 A large number of observations exist for the tropical and temperate oceans (Figure 4), particularly
353 in the 30-40°N band where rates were measured in offshore waters of Georgia and California
354 (Tolar et al., 2020; Liu et al., 2018). Ammonia oxidation rates vary from <0.01 to over 1000 nmol
355 N L^{-1} d^{-1} with a median value of 7.7±9.8 nmol N L^{-1} d^{-1}. There is no clear latitudinal trend in the
356 ammonia oxidation rates. In contrast, Clark et al. (2022) found higher ammonia oxidation rates in
357 the southern hemisphere along the north-south transect in the Atlantic Ocean. This latitudinal
358 pattern is hypothesized to be explained by the difference in the supply of dissolved organic
359 nitrogen (DON) by lateral transport into the gyre interior from the eastern boundary upwelling
360 (Clark et al., 2022). The stimulation of ammonia oxidation rates by a lateral DON supply has also
361 been observed in the Western Pacific (Xu et al., 2018).

362

363
364 Figure 5. Monthly variation (1-12: January to December) of ammonia oxidation observations (a)
365 and ammonia oxidation rates (b-c) divided into observations taken in the Northern Hemisphere
366 (left panels) and Southern Hemisphere (right panels). Jitter according to data density is added in
367 subplot b.

368

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

377

378

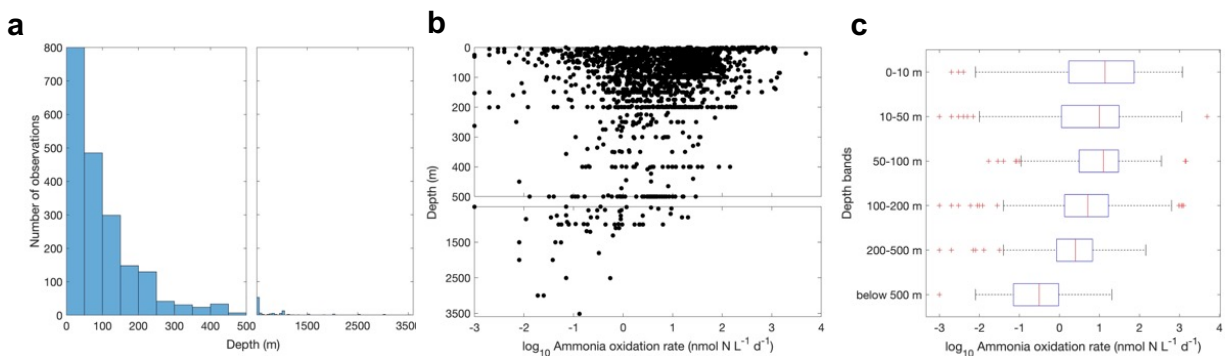
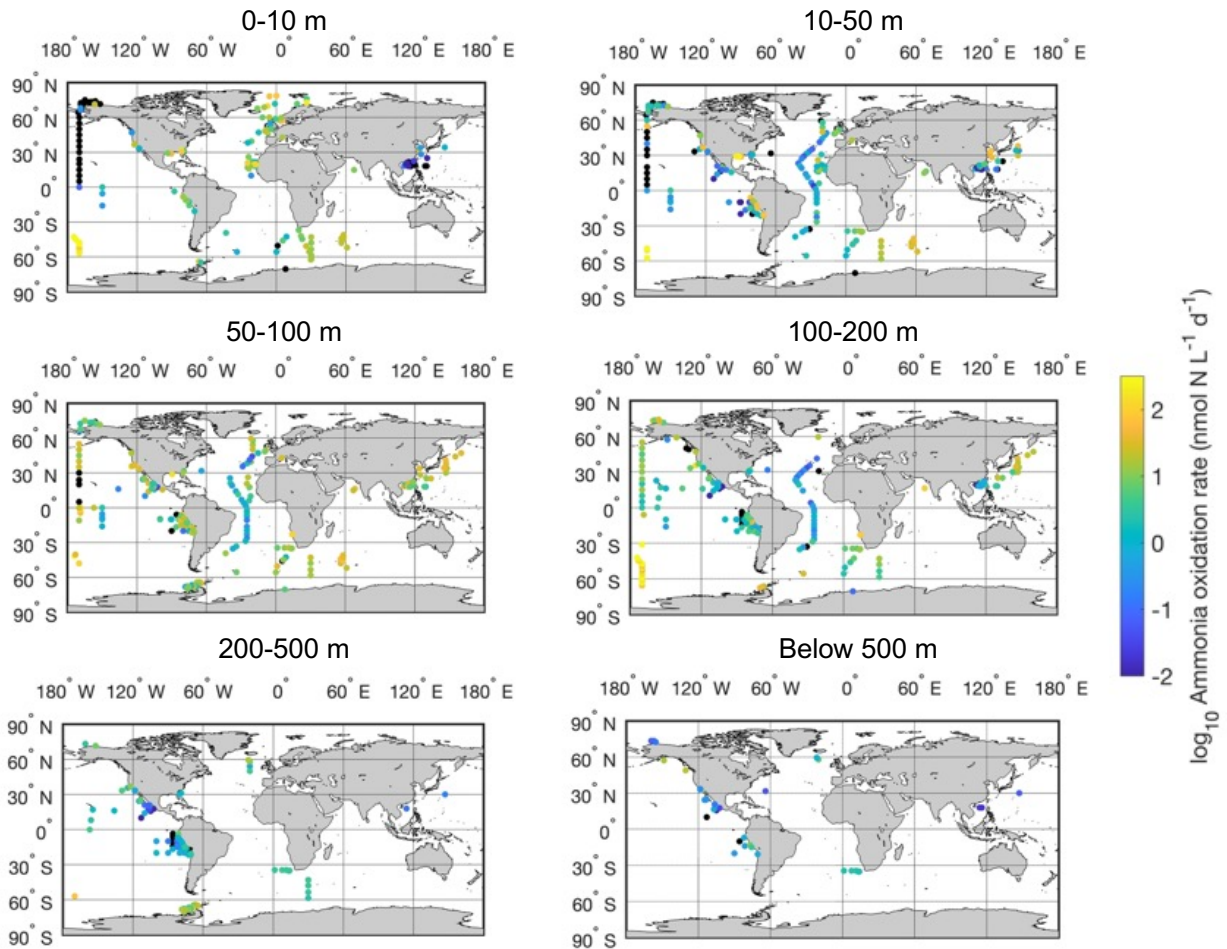



Figure 6. Vertical variation of ammonia oxidation observations (a) and ammonia oxidation rates
(b-c). Note the axis breaks at 500 m depth in subplots a and b.

381

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

391

392

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

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

395

396 There is a large spatial and vertical variation in ammonia oxidation rates (Figure 7). Some hotspots

397 with rates >100 nmol N L^{-1} d^{-1} include the subpolar North Atlantic (Clark et al., unpublished),

398 Southern Ocean (Mdutyana et al., 2020), and coastal waters off California and Georgia (Tolar et

399 al., 2020; Liu et al., 2018). Particularly, there are extremely high ammonia oxidation rates >1000

400 nmol N L^{-1} d^{-1} observed in the surface Pacific Southern Ocean (Raes et al., 2020), deserving further

401 studies to confirm this pattern. In contrast, some low rates <0.01 nmol N L^{-1} d^{-1} or rates below the

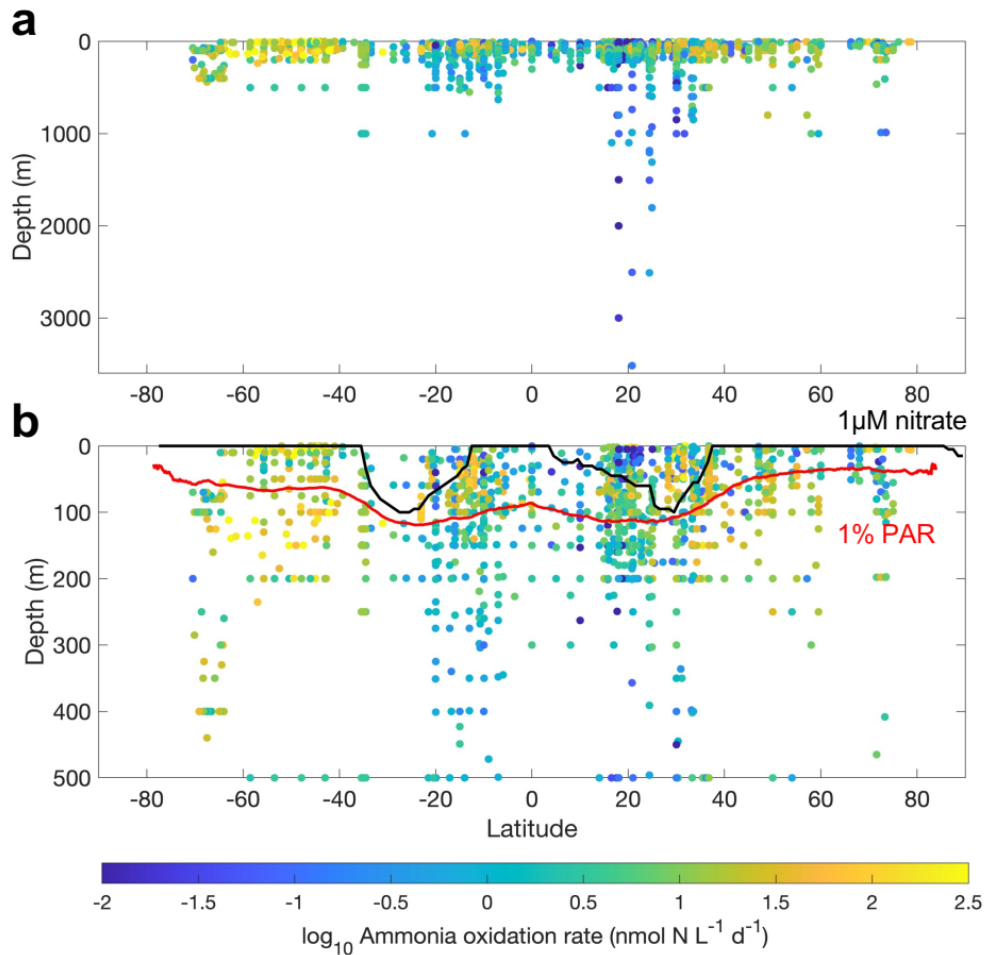
402 detection limit are found in the surface sunlit North Pacific, which is likely caused by the light

403 limitation of nitrifiers, and nitrifier competition with phytoplankton for NH_4^+ in well-lit areas

404 (Smith et al., 2014). For example, peak ammonia oxidation rates are often found in regions/depths

405 where NO_3^- is present or light levels are low such that competition of nitrifiers with phytoplankton

406 for NH$_4^+$ diminishes (Figure 8; Wan et al., 2021). Additionally, low rates are found in oxygen-
407 depleted waters of the eastern tropical Pacific where ammonia oxidation is likely limited by
408 oxygen availability (Peng et al., 2016).

409

410

411 Figure 8. Latitudinal and vertical distribution of ammonia oxidation rates in the whole water
412 column (a) and from the top 500 m (b). The climatological depths of the euphotic zone (1% PAR)
413 obtained from MODIS satellite observations and 1 μM nitrate obtained from World Ocean Atlas
414 2018 (García et al., 2019) are shown by the red line and black lines, respectively.

415

Distribution of nitrite oxidation

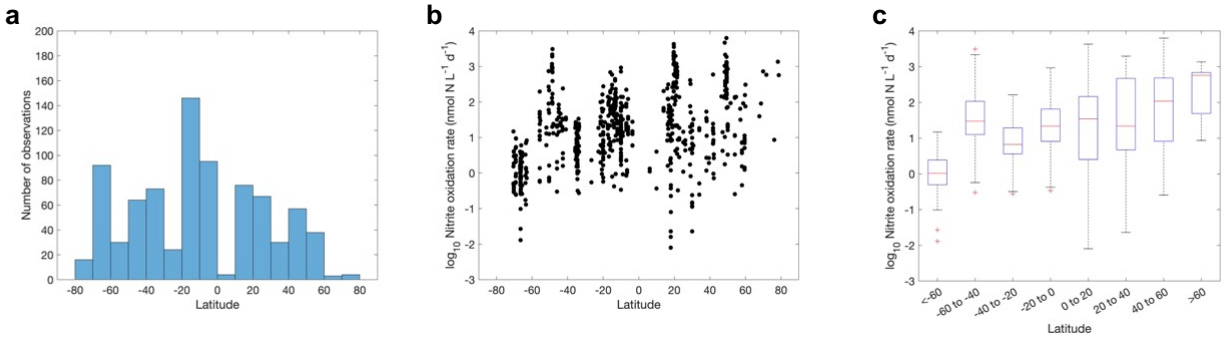



Figure 9. Number of nitrite oxidation observations (a) and nitrite oxidation rates (b-c) within latitudinal bands.

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

432

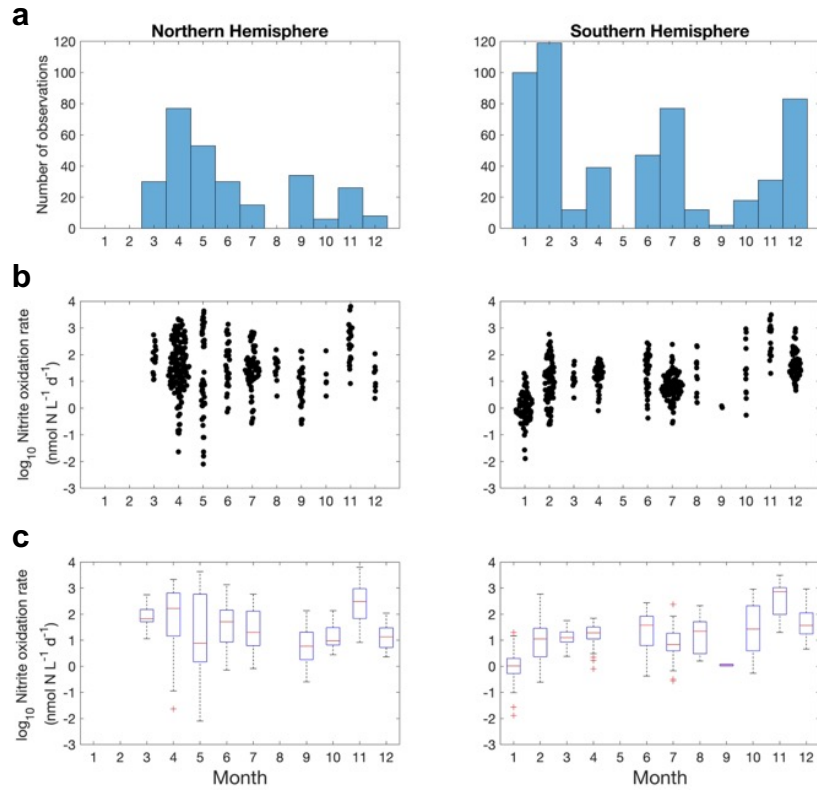
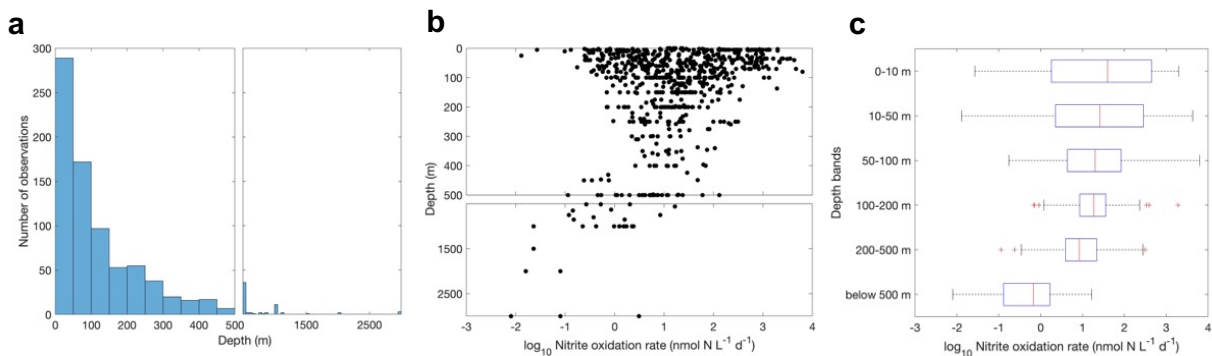



Figure 10. Monthly variation (1-12: January to December) in the number of nitrite oxidation observations (a) and nitrite oxidation rates (b-c).

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

443

444 Figure 11. Vertical variation of nitrite oxidation observations (a) and nitrite oxidation rates (b-c).

445 Note the axis breaks at 500 m depth in subplots a and b.

446

447 Most of the nitrite oxidation rates were also measured at depths shallower than 500 m, accounting

448 for ~94% of the total measurements (Figure 11). There is a large spatial variation in the nitrite

449 oxidation observations and rates (Figure 12). Observations are lacking in the central Pacific Ocean

450 and Indian Ocean outside of the oxygen minimum zones. Nitrite oxidation rates decrease with

451 depth. Globally, the highest median nitrite oxidation rates were found in the surface water (0-10

452 m layer), which is mainly attributed to the high surface rates observed over the United Kingdom

453 shelves, subpolar North Atlantic and Mauritanian upwelling system (Figure 12; Clark et al.,

454 unpublished; Clark et al., 2016). After removing these high surface nitrite oxidation rates, the depth

455 profiles of nitrite oxidation often show a subsurface maximum that is slightly deeper than the

456 subsurface maximum of ammonia oxidation (Figure 13). This difference may be related to the

457 higher sensitivity of nitrite oxidizers/nitrite oxidation to light (Wan et al., 2021; Olson, 1981b).

458 Interestingly, some deep peaks of nitrite oxidation rates have been found in the oxygen-depleted

459 waters in the oxygen minimum zones (Peng et al., 2015; Babbin et al., 2020; Ward et al., 1989;

460 Beman et al., 2013). These high rates stand out in depths below the 1 µM nitrate threshold and

461 above the 1% PAR level between 20°N and 20°S (Figure 14). Many hypotheses (Sun et al., 2023)

462 have been proposed to explain the observed "anaerobic" nitrite oxidation, including alternative

463 oxidants like iodate (Babbin et al., 2017), distinct nitrite oxidizers that are only present in the

464 OMZs and adapted to the low oxygen conditions (Sun et al., 2021), nitrite dismutation ($2H^+ +$

465 $5NO_2^- \rightarrow N_2 + 3NO_3^- + H_2O$; van de Leemput et al., 2011; Babbin et al., 2020; Tracey et al., 2022),

466 and oxygen intrusions (Buchanan et al., 2023). Whether nitrite oxidation is truly anaerobic and

467 how nitrite oxidation is sustained in oxygen depleted waters remain to be determined.

468

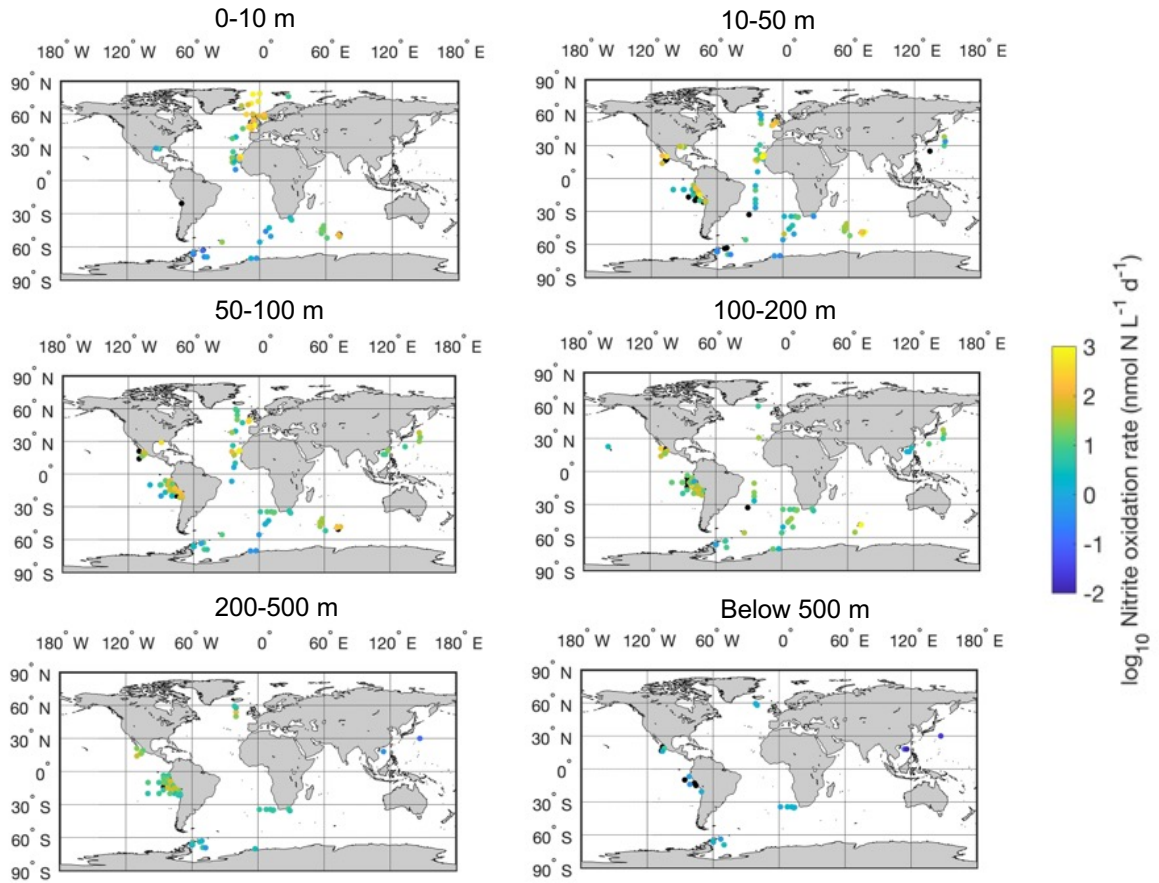
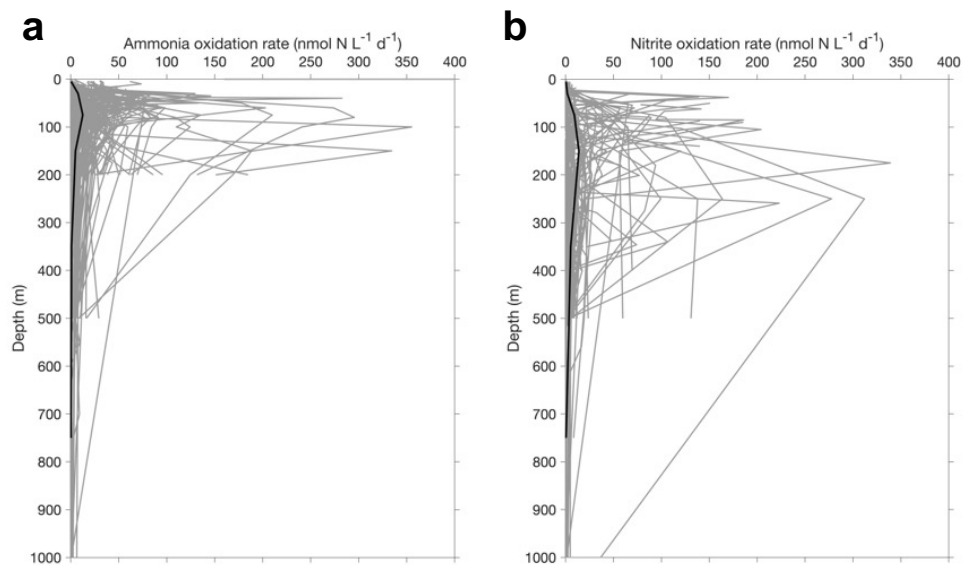



Figure 12. Spatial distribution of nitrite oxidation rates in six depth intervals in the global ocean.

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

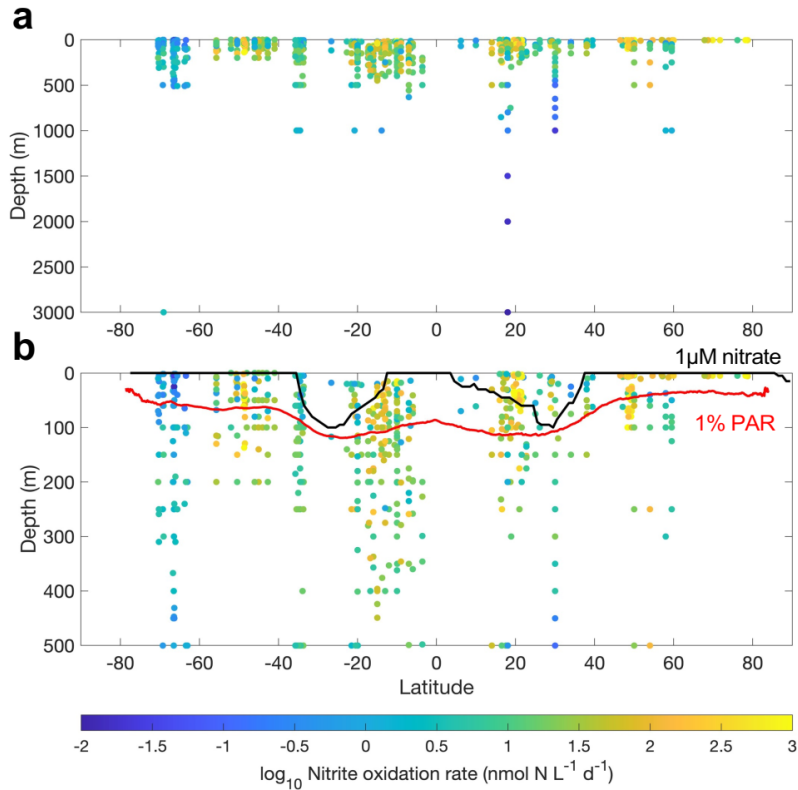
472

473

474 Figure 13. Depth profiles of ammonia oxidation (a) and nitrite oxidation (b) in the top 1000 m.

475 Only depth profiles with five or more measurements/depths are included in this figure. The median

476 profiles of ammonia oxidation and nitrite oxidation are shown in thick black lines, showing the

477 maximum of nitrite oxidation deeper than the maximum of ammonia oxidation.

478

479

480 Figure 14. Latitudinal and vertical distribution of nitrite oxidation rates in the whole water column

481 (a) and from the top 500 m (b). The lower panel shows data from the top 500 m. The climatological

482 depth of the euphotic zone (1% PAR) and 1 μM nitrate are shown by the red and black lines

483 respectively.

484

485

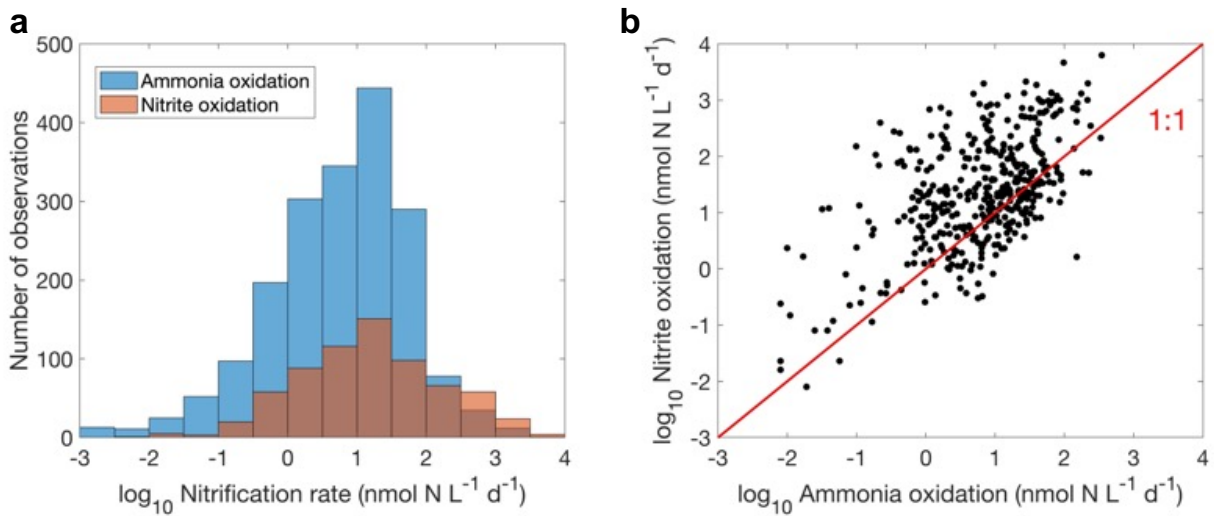
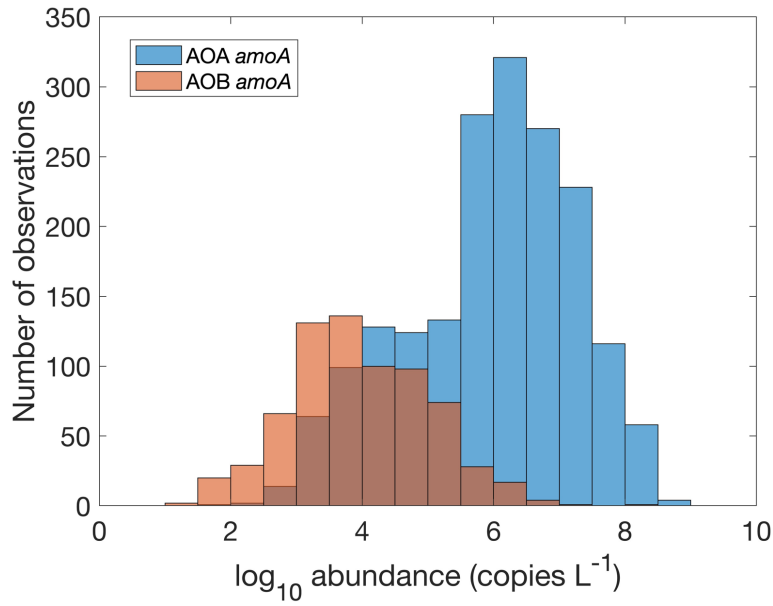



Figure 15. Comparison between ammonia oxidation and nitrite oxidation. (a) Histogram of both rates globally. Note the colors change slightly where they overlap in the histograms. (b) Relationship between ammonia oxidation and nitrite oxidation measured at the same locations and time (y=0.62*x+0.82, r = 0.54, p < 0.01).

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

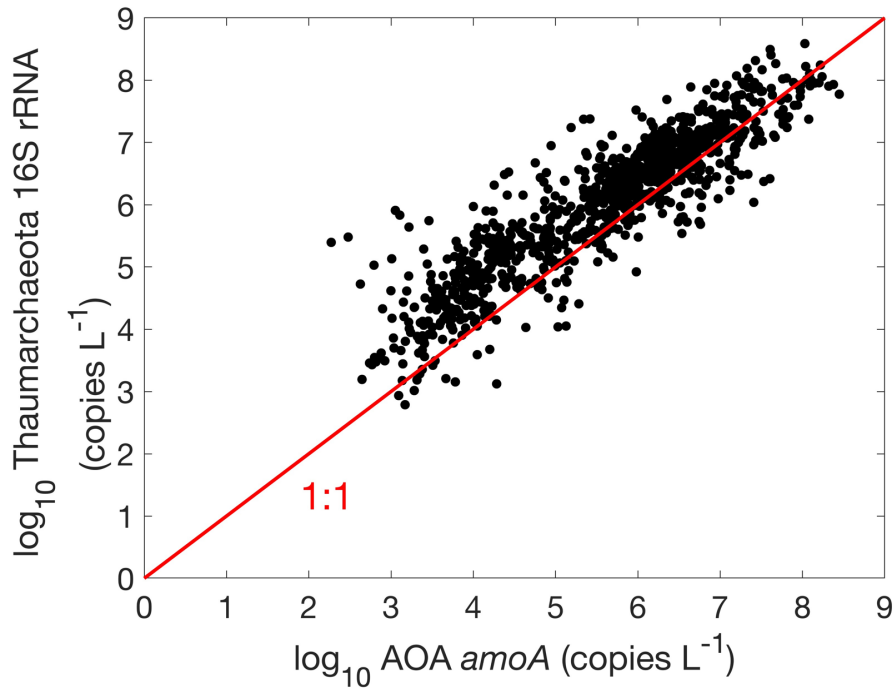
Distribution of ammonia oxidizers

505

506

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

508 represent the total abundance of archaeal *amoA* gene abundance or the sum of WCA and WCB.

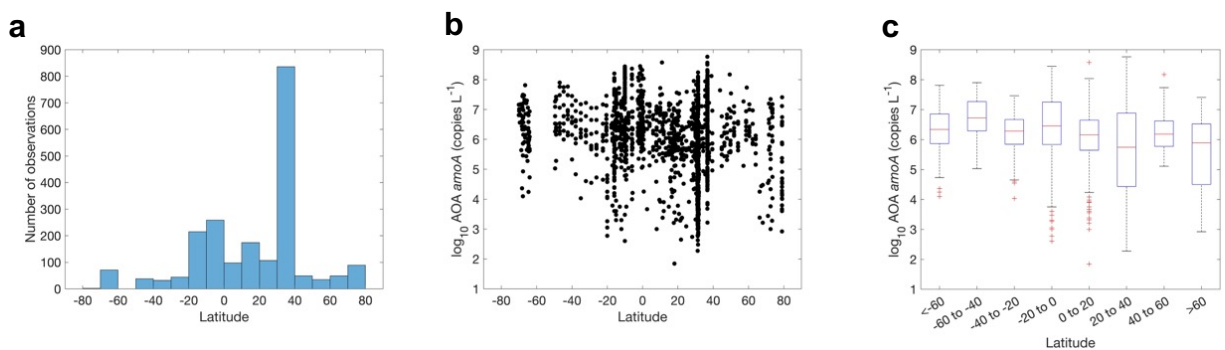
509 Note the colors change slightly where they overlap in the histograms.

510

511

512 Figure 17. Comparison between AOA *amoA* and *Thaumarchaeota* 16S rRNA gene abundances
513 (y=0.78*x+1.66, r = 0.9, p < 0.01).

514

515 There are 1893, 892, 1073 measurements of the abundance of AOA *amoA* gene, AOB *amoA* and
516 16S rRNA of *Thaumarchaeota*, respectively. Within the measurements of AOA *amoA* abundance,
517 1204 and 1101 measurements were separately conducted for water column ecotype A (WCA)
518 *amoA* and water column ecotype B (WCB) *amoA*. Thus, the total *amoA* gene abundance was
519 calculated by summing the abundance of WCA and WCB when available. The AOA *amoA*
520 abundance with median of 1.34 x 10^6 copies L^{-1} is substantially higher than AOB *amoA* gene
521 abundance with median of 7.96 x 10^3 copies L^{-1} (Figure 16), confirming the dominance of archaeal
522 ammonia oxidizers in the ocean. We also found that *Thaumarchaeota* 16S rRNA gene abundance
523 positively correlates with but slightly outnumbers the *amoA* gene abundance (Figure 17). This may
524 suggest that not all the *Thaumarchaeota* contain the *amoA* genes to oxidize NH$_4^+$ or some
525 organisms containing *amoA* genes (such as the *Nitrosopumilus*-like group) may have been missed
526 due to primer bias (Sintes et al., 2016; Hiraoka et al., preprint), Since total AOA *amoA* genes have
527 the largest number of observations and better represent ammonia oxidation capability, we will use
528 it to show the spatial and vertical distribution of ammonia oxidizer abundance.

529

530
531 Figure 18. Number of observations of archaeal ammonia oxidizers (a) and the abundance of
532 archaeal ammonia oxidizers (b-c) within latitudinal bands.

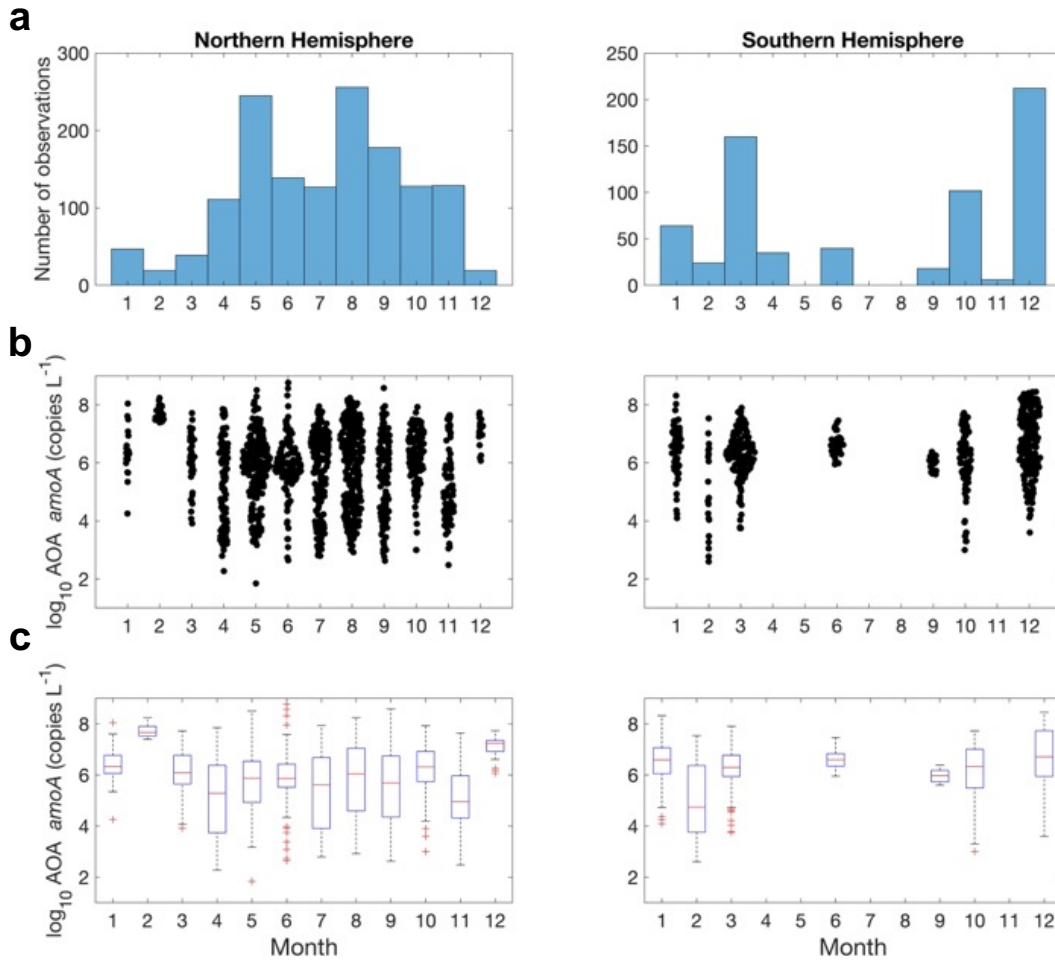
533

534 The eastern Pacific Ocean and Atlantic Ocean have the majority of the observations for ammonia
535 oxidizers, particularly in the 30-40°N band where ammonia oxidizers were measured in the coastal
536 waters off California and Georgia (Liu et al., 2018; Tolar et al., 2020). In contrast, observations in

537 the Indian Ocean and Southern Ocean are scarce. The AOA *amoA* gene abundance varies from a

538 few copies per liter in the surface ocean to over 10^8 copies L^{-1} in the subsurface of equatorial

539 Atlantic. There is no clear latitudinal trend in the abundance of ammonia oxidizers.

540

541

542 Figure 19. Monthly variation (1-12: January to December) in the number of the observation (a)

543 and abundance (b-c) of archaeal *amoA*.

544

545 There are substantially more observations in the northern hemisphere than the southern

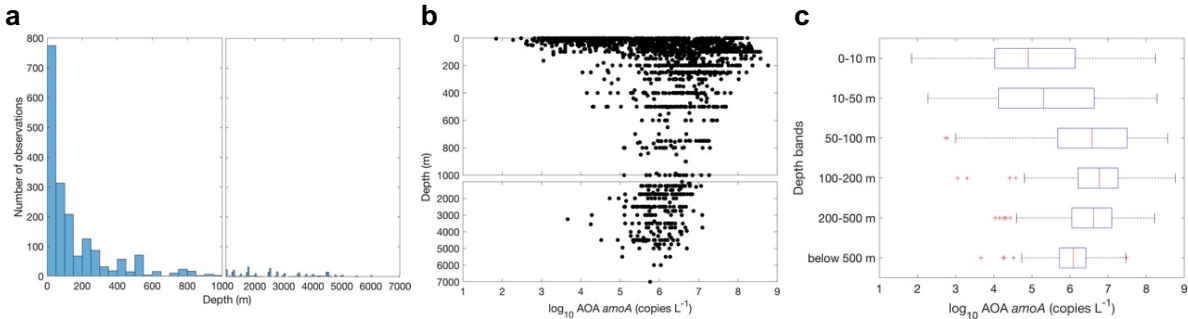
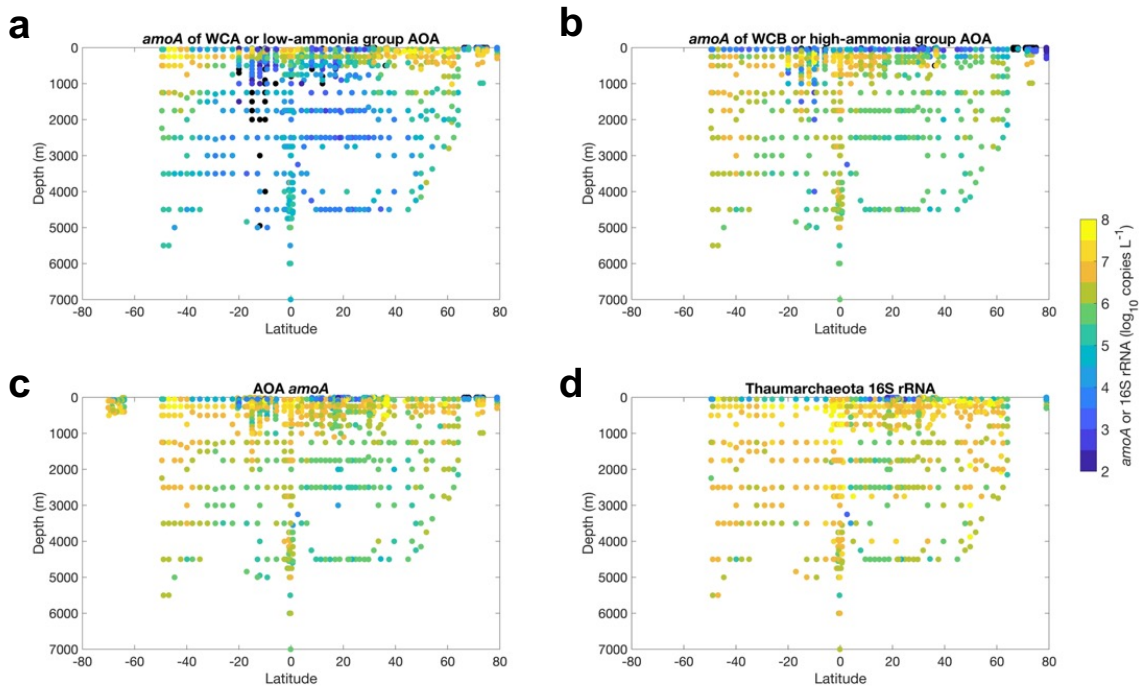
546 hemisphere. We do not see a clear seasonal trend in nitrifier abundance due to the large monthly

547 variation. A time-series study in the Monterey Bay shows that seasonality can be observed for the

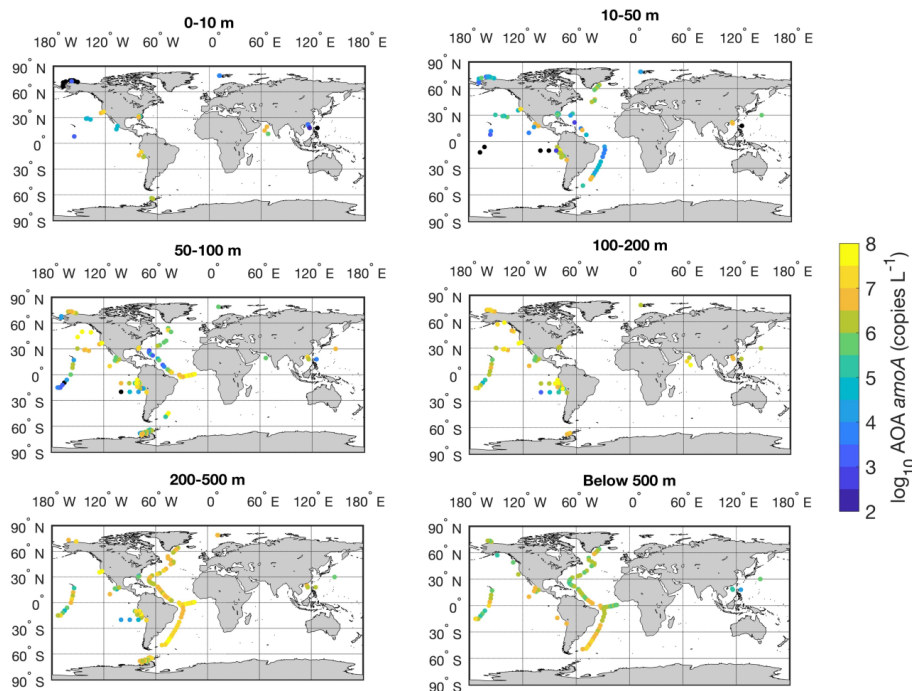
548 top 200 m while the overall community of ammonia oxidizers was stable at 500 m (Tolar et al.,

549 2020). In addition, mid-summer peaks in *Thaumarchaeota* abundance have been observed at the

550 coast off Georgia (Hollibaugh et al., 2013). More time-series studies with high-frequency sampling

551 would be useful for characterizing the response of the nitrifier community to seasonal changes in
552 environmental drivers.
553

554
555 Figure 20. Vertical distribution of archaeal *amoA* observations (a) and archaeal *amoA* gene
556 abundance (b-c). Note the axis breaks at 1000 m depth in subplots a and b.
557

558
559 Figure 21. Vertical distribution of AOA *amoA* gene abundance (a-c) and 16S rRNA of
560 *Thaumarchaeota* (d) across the latitudinal gradient. WCA and high-ammonia concentration groups
561 (a) are shown together while WCB and low-ammonia concentration groups (b) are shown together.
562 The total AOA *amoA* or the sum of WCA and WCB is shown in (c).
563

564 Most of the abundance measurements of ammonia oxidizers were made in the top 1000 m (Figure
565 20). Median ammonia oxidizer abundance increases from ~10^5 copies L^{-1} in the 0-10 m depth layer
566 to ~10^7 copies L^{-1} in the 100-200 m layer, then decreases with depth and remains relatively
567 constant at ~10^6 copies L^{-1} in the deep ocean below 500 m depth. We noticed that *amoA* abundance
568 and ammonia oxidation rates appear to have different depth distributions, particularly for the top
569 200 m (Figure 6c and Figure 20c): *amoA* abundance in 0-10 m layer is lower than in 100-200 m
570 layer while ammonia oxidation rates in 0-10 m layer are comparable to the rates observed in 100-
571 200 m layer. These distributions may suggest depth differences in cell-specific activity which
572 might be interesting for future investigation. The archaeal *amoA* is sometimes quantified separately
573 for two ecotypes including water column groups A and B. Water column group A dominates the
574 upper 200 meter while water column group B is more abundant in the mesopelagic and
575 bathypelagic deep ocean below 500 m (Figure 21), likely reflecting their different affinities for
576 NH_4^+ (Beman et al., 2008; Sintes et al., 2016). The vertical distribution of ammonia oxidizers is
577 similar to the vertical distribution of ammonia oxidation rates (Figure 13).

578

579
580 Figure 22. Spatial distribution of AOA *amoA* gene in six depth intervals in the global ocean.
581 Locations with abundance below the detection limit are shown in the black circles.

582

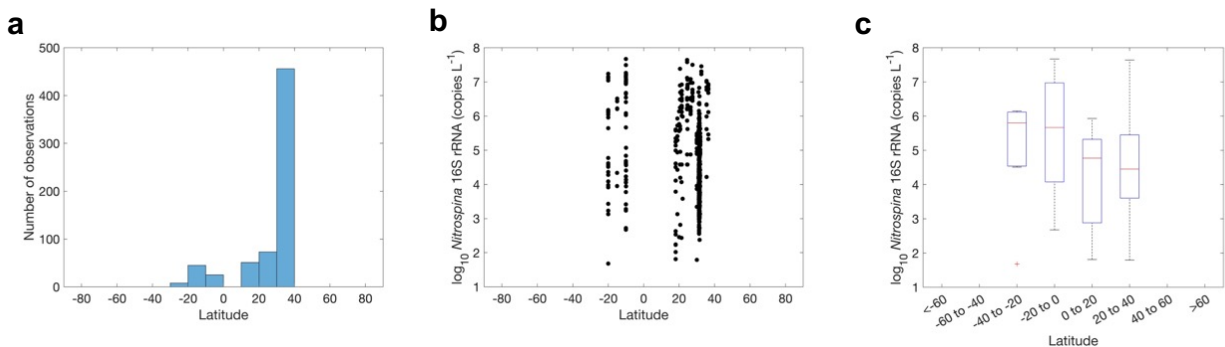
583 There is a large spatial variation in the abundance of ammonia oxidizers (Figure 22). High
584 abundances are found in the tropical Atlantic and eastern tropical Pacific where upwelling drives
585 high rates of marine primary production. In contrast, some of the lowest abundances of ammonia
586 oxidizers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

590

Distribution of nitrite oxidizer abundance

591 **Distribution of nitrite oxidizer abundance**

592 There are only seven studies available reporting the abundance of nitrite oxidizers in the ocean.
593 One study used the *nxr* marker gene and the other six studies used 16S rRNA gene of either
594 *Nitrospina* or *Nitrospira*. Since *Nitrospina* is the dominant nitrite oxidizer in the ocean (Beman et
595 al., 2013; Pachiadaki et al., 2017) and accounts for most of the observations, we use it to show the
596 distribution of nitrite oxidizers.

597

598

599 Figure 23. Number of observations (a) and abundance (b-c) of *Nitrospina* within latitudinal bands.

600

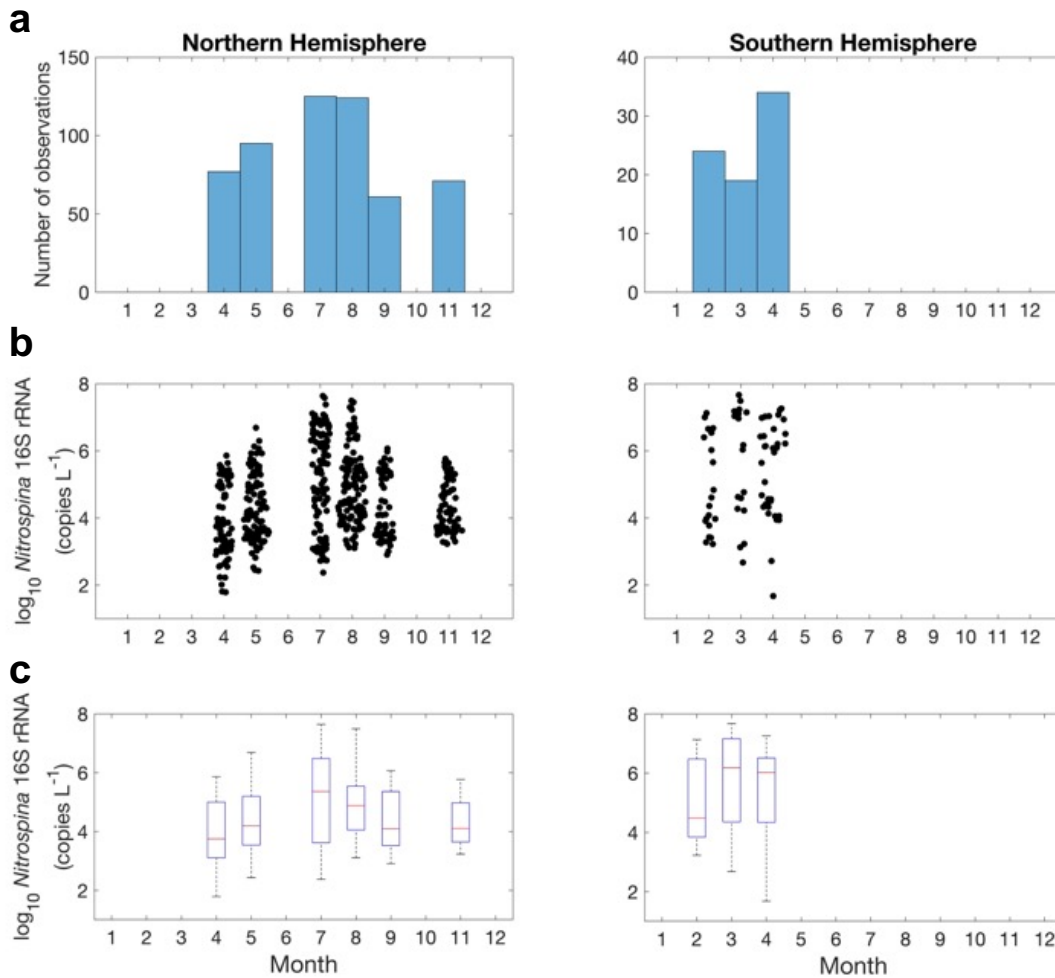
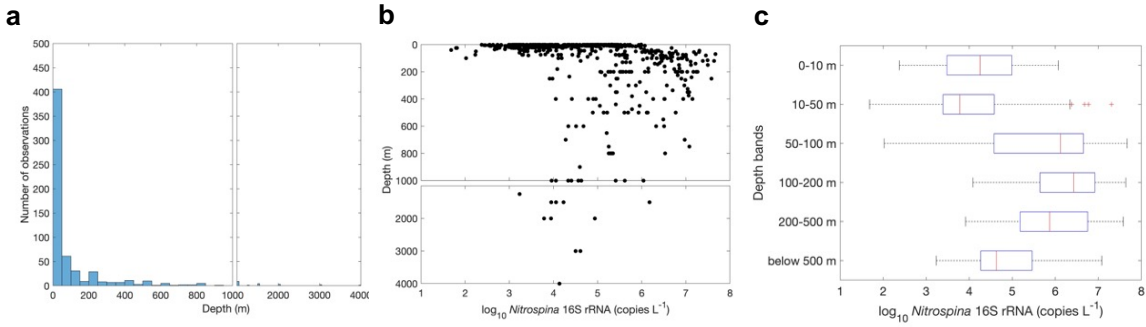



Figure 24. Monthly variation (1-12: January to December) in the number of observations (a) and abundance (b-c) of *Nitrospina*.

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

612

613 Figure 25. Vertical distribution of *Nitrospina* observations (a) and gene abundance (b-c). Note the

614 axis breaks at 1000 m depth in subplots a and b.

615

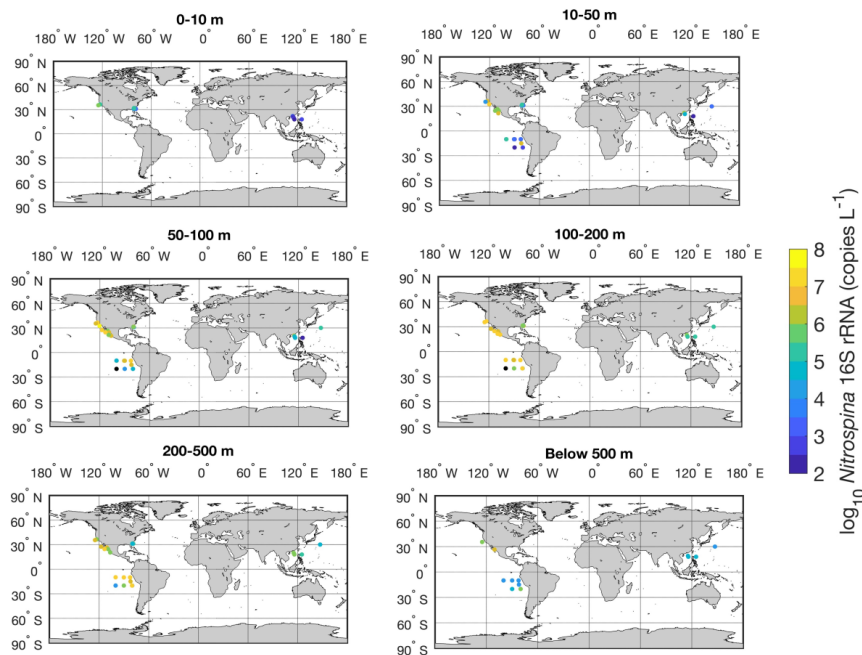
616 The vertical distribution of nitrite oxidizers resembles the vertical distribution of ammonia

617 oxidizers: increases from ~10^4 copies L^{-1} in the surface 0-10 m depth layer to a maximum of ~10^6

618 copies L^{-1} in the 100-200 m layer, then decreases to ~$10^{4.5}$ copies L^{-1} in the deep ocean below 500

619 m (Figures 25-26). However, data below 500 m are insufficient to describe the distribution of

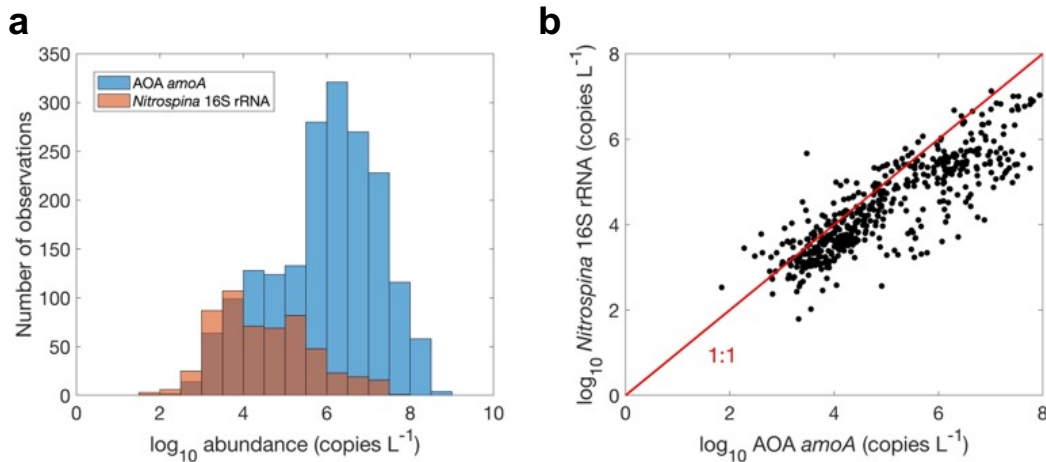
620 nitrite oxidizers in the deep ocean. The vertical distribution of nitrite oxidizers qualitatively

621 matches the vertical distribution of nitrite oxidation rates (Figure 13).

622

623

624 Figure 26. Spatial distribution of *Nitrospina* in six depth intervals in the global ocean. Locations

625 with abundances below the detection limit are shown in the black circles.

626

628 Figure 27. Comparison between the number of observations (a) and the correlation between the
629 abundance (b) of the archaeal *amoA* gene and *Nitrospina* 16S rRNA gene (y=0.68*x+1, r = 0.85,
630 p < 0.01). Note the colors change slightly where they overlap in the histograms.

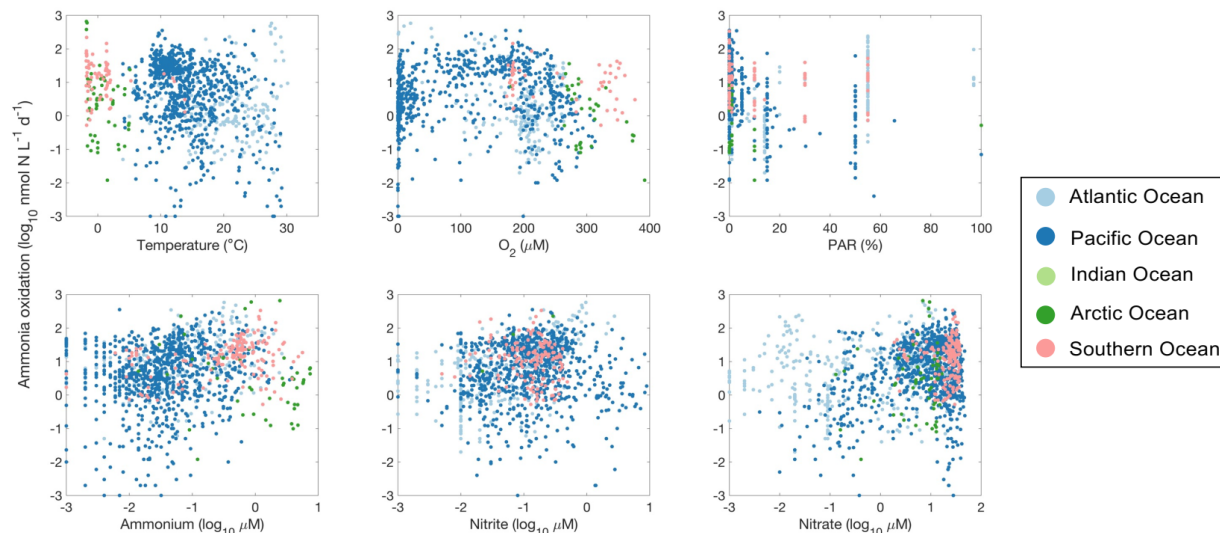
631

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

640

Environmental controls on nitrification rates and the abundance of nitrifiers

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

648

649

650   Figure 28. Relationship between ammonia oxidation rates and environmental factors observed in

651   different ocean basins.

652

653   Ammonia oxidation rates showed a weak negative correlation with temperature ($r = -0.22$, $p <$

654   0.01; Figure 28). Some of the high rates are found below 0ºC, and at around 10ºC and 25ºC.

655   Temperature manipulation experiments showed varying temperature sensitivity of ammonia

656   oxidation in different regions or among natural assemblages (Baer et al., 2014; Horak et al., 2018;

657   Zheng et al., 2020). The highest ammonia oxidation rates were found in the oxygen range between

658   100 and 200 μM ($p > 0.01$). But ammonia oxidation has also been detected in low oxygen waters

659   (e.g., <10 μM) in the oxygen minimum zones (Bristow et al., 2016a; Peng et al., 2015), reflecting

660   the high affinity of ammonia oxidizers for oxygen. Oxygen production by ammonia-oxidizing

661   archaea may support their presence and activity in the oxygen minimum zones (Kraft et al., 2022).

662   Ammonia oxidation generally decreases at relatively high light intensity (PAR% relative to surface

663   PAR) due to light inhibition and substrate competition with phytoplankton (but the negative slope

664   is not significant, $p > 0.01$). Nevertheless, high ammonia oxidation rates have been measured in

665   the euphotic zone at 55% PAR in the Atlantic Ocean (Clark et al., 2008; Clark et al., unpublished).

666   Although light manipulation experiments have shown clear light inhibition of nitrification rate at

667   specific locations (e.g., Xu et al., 2019; Shiozaki et al., 2019), the relationship between nitrification

668   and light intensity is ambiguous at the global scale, which may be related the compounding factors

669   on nitrification. For example, the covarying ammonium availability would complicate the impact

670   of change in light intensity. Ammonia oxidation increases with N nutrient concentration ($p < 0.01$).

671   NH_4^+ is the substrate while NO_2^- is the product of ammonia oxidation. The Michaelis-Menten-like

672   kinetics of ammonia oxidation rate have been observed in various ocean regions (Frey et al., 2022;

673   Newell et al., 2013; Horak et al., 2013; Xu et al., 2019; Zhang et al., 2020; Mdutyana et al., 2022a

674   and b). High concentrations of NH_4^+ and NO_2^- likely reflect intense recycling of organic matter

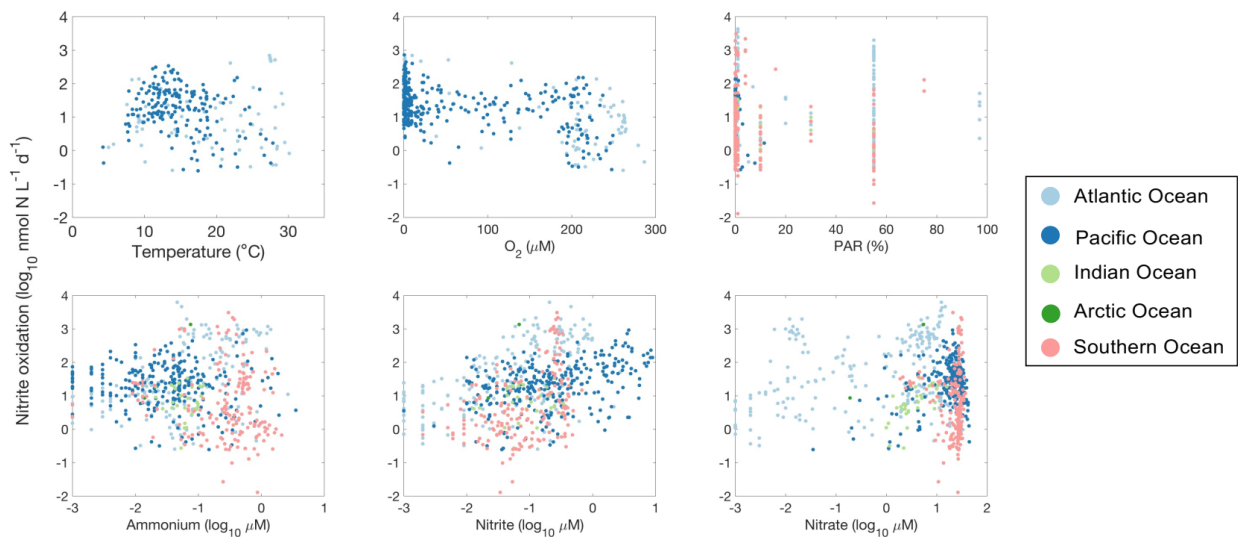
675   and remineralization. The presence of high NO_3^- concentration may relieve the competition

676   between ammonia oxidizers and phytoplankton for NH_4^+, therefore leading to high ammonia

677   oxidation rates (Wan et al., 2018). In addition, recent studies have shown that AOA have a high

678   requirement for iron and copper, which may affect the distribution of nitrification in the ocean

679   (Shafiee et al., 2019; Shafiee et al., 2021).

680

681

682   Figure 29. Relationships between nitrite oxidation rates and environmental factors observed in

683   different ocean basins.

684

685   High nitrite oxidation rates are found between 10°C and 20°C (Figure 28). Surprisingly, some of

686   the highest nitrite oxidation rates were measured in the oxygen minimum zones even with oxygen

687   levels below detection limits (Ward et al., 1989; Sun et al., 2017; Sun et al., 2021). Nitrite oxidation

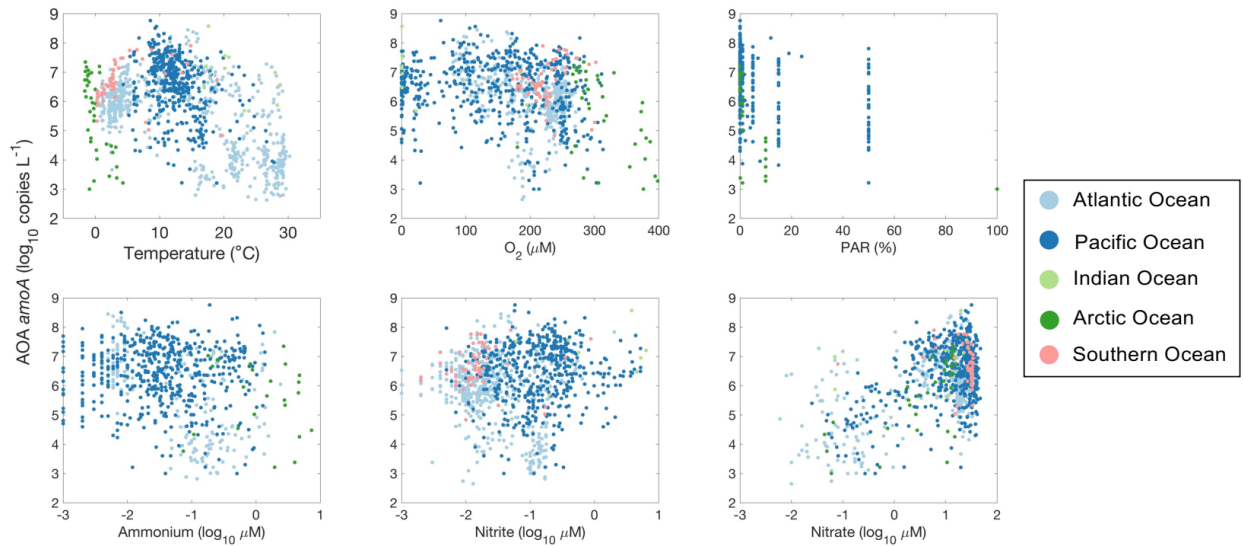
688   in anoxic waters has been observed to be inhibited (Sun et al., 2017) or stimulated (Bristow et al.,

689   2016a) by the addition of oxygen. The mechanisms for apparently anaerobic nitrite oxidation

690   remain to be determined (Sun et al., 2023). Similar to ammonia oxidation, nitrite oxidation is often

691   reported to be inhibited by high light levels, but the relationship is not statistically significant

692   across the database ($p > 0.01$; Figure 29) partly due to the presence of high nitrite oxidation rates

693 in the euphotic zone (e.g., Clark et al., 2016). High nitrite oxidation rates are often observed in
694 regions with high NO_2^- concentration ($r = 0.23$, $p < 0.01$). For example, the highest nitrite oxidation
695 rates were observed at NO_2^- concentrations near 0.5 μM (Figure 29).
696

697

698 Figure 30. Relationship between archaeal *amoA* gene abundance and environmental factors
699 observed in different ocean basins.

700

701 We use *amoA* gene abundance to represent the abundance of ammonia oxidizers with the caveat
702 that the number of gene copies may not equal the cell numbers. Ammonia oxidizers are adapted to
703 a wide range of environmental conditions (Figure 30). Their abundance reaches a maximum at
704 around 10°C. Ammonia oxidizers are also present in low oxygen waters and the euphotic zone
705 with slightly lower abundance. Interestingly, ammonia oxidizers show relatively constant
706 abundance across the NH_4^+ concentration gradient while ammonia oxidation rates are low under
707 low NH_4^+ concentration (e.g., <0.01 μM). A large portion of the *amoA* observations were
708 conducted in the deep ocean where nitrate concentration was above 10 μM. Some of the highest
709 *amoA* abundance were found in these NO_3^- enriched waters.

710

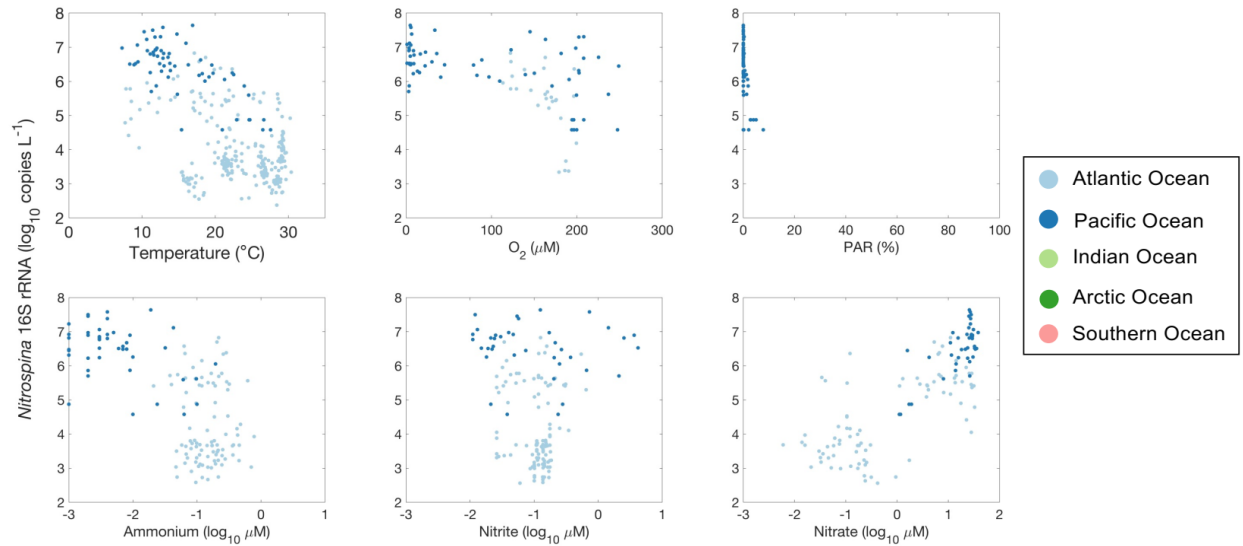



Figure 31. Relationships between *Nitrospina* 16S rRNA gene abundance and environmental factors observed in different ocean basins.

It is difficult to evaluate the relationship between nitrite oxidizers and environmental factors due to the limited number of observations (Figure 31). Nevertheless, one interesting pattern is the presence of high *Nitrospina* abundance in oxygen depleted waters. The nitrite oxidizers present in the oxygen depleted waters are distinct from those found in oxygenated waters or currently cultivated strains (Sun et al., 2019; Sun et al., 2021). Similar to *amoA* abundance, *Nitrospina* 16S rRNA gene abundance also increased with NO_3^- concentration.

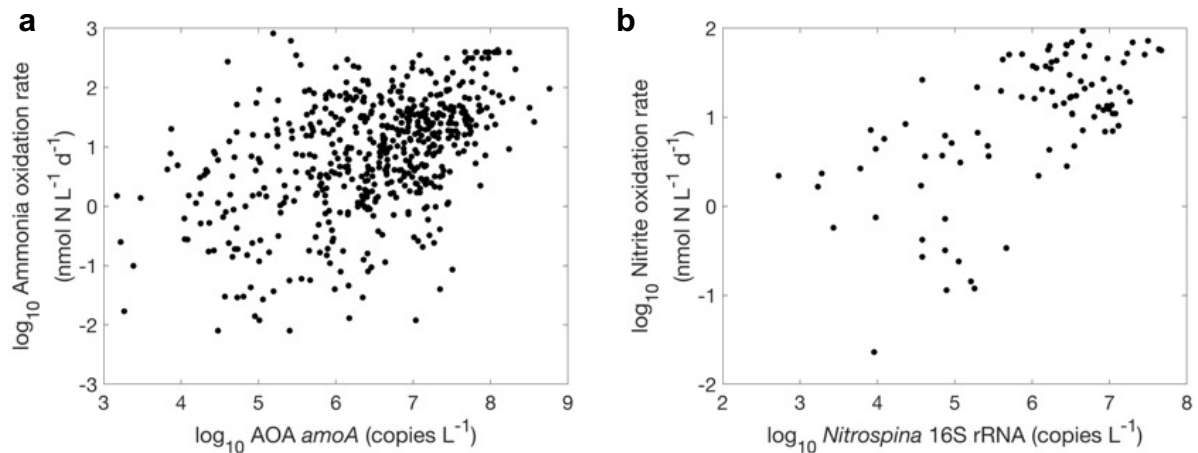



Figure 32. Relationships between nitrifier abundance and nitrification rate. (a) ammonia oxidation vs AOA *amoA* gene abundance (y=0.43*x-1.92, $r = 0.46$, $p < 0.01$); (b) nitrite oxidation vs *Nitrospina* 16S rRNA gene abundance (y=0.45*x-1.65, $r = 0.65$, $p < 0.01$).

There is a positive correlation between AOA *amoA* gene abundance and ammonia oxidation rates ($r = 0.46$, $p < 0.01$), and between *Nitrospina* 16S rRNA abundance and nitrite oxidation rate ($r = 0.65$, $p < 0.01$) (Figure 32) even though the correlation is weak. This lack of a strong relationship has also been found in regional studies (Tolar et al., 2020), which may be caused by the perturbation of the microbial community during rate measurement incubations. Furthermore, the addition of nitrogen substrate during rate measurement incubations may stimulate the growth of nitrifiers and the subsequently measured nitrification rate. Overall, using functional gene abundances to predict their functional activity needs to be conducted with caution since the presence of genes only reflects the functional potentials.

Applications of the database and suggestions for future research

This database will be useful for a broad scientific community who are interested in marine biogeochemistry and marine microbial ecology. Potential applications include but are not limited to: 1) Compare future measurements of nitrification rates or nitrifier abundance in a specific region to previous measurements conducted in the same regions, and contextualize new measurements at the global scale. 2) Meta-analysis of environmental controls on the distribution of nitrification and nitrifier abundance at regional and global scales. The simple correlation analyses provided here only considered individual environmental drivers separately while other drivers are changing simultaneously. Analysis with environmental assemblages could complement laboratory culture experiments. 3) Help to validate and improve model parametrization of nitrification and nitrifiers. For example, ammonia oxidation has been modeled as a function of substrate concentration and specific ammonia oxidation rate (Yool et al., 2007). However, nitrification has been found to be regulated by temperature, oxygen, light and many other environmental factors that are not considered in that model. A better representation of nitrification in ocean biogeochemical models could help to constrain the estimates of marine new production, N_2O production and many other key processes. 4) Guide future nitrification studies, e.g., conducting measurements in poorly sampled regions or seasons.

754

755   Based on the historical measurements of nitrification and nitrifiers, we provide recommendations

756   for future research below.

757

758   1. Method standardization is useful for comparison among studies. Nitrification has been mostly

759   measured by ^{15}N substrate tracer addition and product dilution methods. The ^{15}N product dilution

760   method tends to yield higher rates relative to the ^{15}N substrate tracer addition method (Figure 1).

761   This is perhaps to be expected since the ^{15}N product dilution method measures all the NO_2^-

762   production pathways including ammonia oxidation (and organic N oxidation) and nitrate reduction

763   instead of only NO_2^- production from ammonia oxidation as is measured by the $^{15}NH_4^+$ tracer

764   addition method. Comparison between different methods should be conducted to resolve the

765   difference or even correct some of the previous measurements.

766

767   Additionally, the amount of tracer added should be recorded and reported because the increased

768   substrate concentration may enhance nitrification rate. Therefore, the measured rates should be

769   interpreted as potential rates rather than in-situ rates when the amount of tracer addition is large

770   compared to the ambient substrate concentration. If possible, substrate kinetic experiments should

771   be conducted for in-situ rate calibration (e.g., Wan et al., 2018; Mdutyana et al., 2022a and b).

772

773   The measured product of ammonia oxidation should also be reported (e.g., either only NO_2^- or

774    $NO_2^- + NO_3^-$). When ambient NO_2^- concentration is low, the $^{15}NO_2^-$ produced from $^{15}NH_4^+$ tracer

775   may be further oxidized to $^{15}NO_3^-$. Thus, nitrification may be underestimated if only NO_2^- is

776   measured. Alternatively, NO_2^- carrier may be added into the incubation to 'trap' the produced

777    $^{15}NO_2^-$. In addition to only measuring ammonia oxidation, more observations of nitrite oxidation

778   are desirable to evaluate mechanisms controlling the coupling or decoupling of the two steps of

779   nitrification.

780

781   Furthermore, measurements with at least three time points are preferred during the incubation time

782   courses in order to examine whether the rate has changed during the incubation period. Depending

783   on the incubation period, nitrification rates are reported as either nmol N L^{-1} d^{-1} or nmol N L^{-1} h^{-1}.

784   A conversion factor (e.g., 12 or 24 hours) is required to obtain the same unit. The choice of the

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

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

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

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

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

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

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

Data availability

Data described in this manuscript can be accessed at Zenodo repository under data doi:
https://doi.org/10.5281/zenodo.8355912 (Tang et al., 2023).

846

Conclusions

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

858

Author contributions

860 Weiyi Tang and Bess Ward designed the study with input from Fabien Paulot and Charles Stock.
861 Weiyi Tang compiled the database with data contribution from coauthors, and Weiyi Tang
862 analyzed the database. Weiyi Tang and Bess Ward wrote the manuscript with contribution from
863 coauthors.

864

Competing interests

866 No competing interest is declared.

867

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872 (FWF) project DEPOCA (P 35587-B).

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