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Ammonium and nitrite oxidation in the upper euphotic zone of the oligotrophic Red Sea

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Abstract

Nitrification is widely understood to be inhibited by light in the surface ocean, however, increasing evidence indicates its occurrence at low levels at many sites. The extent to which nitrification remains active in the euphotic zone could have important implications to new production calculations, yet it remains understudied. Here, we quantified ammonium and nitrite oxidation rates in the euphotic zone of the Gulf of Aqaba (Northern Red Sea) from late spring to late summer and examined environmental controls and implications for dark carbon fixation (chemoautotrophy) and new production. Both ammonium and nitrite oxidation were detectable throughout the euphotic zone (~0.1-0.8 nmol N L^{-1} d^{-1}). Overall, rates increased with depth and were strongly suppressed in the highest irradiance surface waters. Integrated rates over the entire euphotic zone (24-56 µmol N m^{-2} d^{-1}) were among the lowest reported for oligotrophic regions globally. This reflects extremely low substrate concentrations and intense, though not complete, photoinhibition. Ammonium and nitrite oxidation together supported <2% of chemoautotrophic activity, suggesting other processes, not accounted for, such as anaplerosis may be important. Depth-resolved correlations with environmental parameters highlight light, temperature, and substrate availability as key regulators of both processes. Our results show that nitrification in the Gulf of Aqaba operates at the lower bounds of global euphotic zone rates and is loosely coupled to carbon cycling. These findings underscore the need to better resolve nitrification dynamics in ultra-oligotrophic, rapidly warming, seas to refine estimates of new production and chemoautotrophic carbon assimilation under future ocean conditions.

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Key words: Ammonia oxidation, Nitrite oxidation, Dark carbon fixation, Red Sea, Oligotrophic.

1 Introduction

Nitrification, the sequential oxidation of ammonium (NH_4^+) to nitrite (NO_2^-) followed by the oxidation of nitrite to nitrate (NO_3^-), is a microbially mediated process central to the regulation of nitrogen availability across nearly all aquatic environments, linking the most reduced and oxidized states of nitrogen (Ward, 2008). Although nitrification does not change the absolute inventory of bioavailable nitrogen (N) in the oceans, it alters the balance among N species that serve as substrates for different organisms, thereby affecting phytoplankton species abundance and growth (Fawcett et al., 2011). Ammonia oxidation is carried out by ammonia-oxidizing archaea and bacteria (Francis et al., 2005; Wuchter et al., 2006), while nitrite oxidation is performed by nitrite-oxidizing bacteria (Mincer et al., 2007; Pachiadaki et al., 2017). Ammonia-oxidizing bacteria that perform the entire process have also been identified in freshwater, terrestrial, and coastal habitats, but have not yet been found in the open ocean (Daims et al., 2015; Fei et al., 2018; van Kessel et al., 2015).

Nitrification has been investigated across a wide range of marine settings, including the Atlantic (Clark et al., 2008, 2022), the Pacific (Wan et al., 2021; Wankel et al., 2007), and the Polar (Mdutyana et al., 2020; Shiozaki et al., 2019) ocean basins, as well as numerous coastal and estuarine systems (Henriksen and Kemp, 1988; Herbert, 1999; Zhu et al., 2018). As a chemoautotrophic process, nitrification contributes to organic carbon production in the ocean interior (Middelburg, 2011; Pachiadaki et al., 2017), and may fuel bacterial carbon demand and support heterotrophic food-webs in the mesopelagic and bathypelagic water depths (Bayer et al., 2024). The activity of nitrifiers is known to be promoted or inhibited by many environmental factors (Ward, 2008), yet specific controls on its occurrence in the water column and broader ecological implications across different ocean settings remain poorly constrained (Tang et al., 2023). Additionally, because uptake of NH_4^+ and NO_3^- has long served to differentiate between 'regenerated' and 'new' production, respectively (Eppley and Peterson, 1979), *in situ* production of NO_3^- by nitrification in the photic zone skews global estimates of new production and carbon export in the oceans (Yool et al., 2007; Wankel et al., 2007).

Here, we report ammonium and nitrite oxidation rates in the euphotic zone (surface and down to ~100 m) of the Gulf of Aqaba (GoA, Northen Red Sea) during late spring and

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throughout the summer season. Rates were compared with common environmental physiochemical and biological parameters to assess drivers of nitrification in this setting. Using these data, we provide estimates of the contribution of ammonium and nitrite oxidation to dark carbon fixation (DCF) and new production in this oligotrophic, warm and well-lit system.

2 Material and methods

Seawater was collected every 20 m throughout the euphotic zone (0-100 m depth) at an offshore, routinely monitored, station in the GoA ("Station A", latitude 29.47 N, longitude 34.92 E). Ammonium and nitrite oxidation rates were assessed using stable ^{15}N isotope enrichment incubations. Five monthly sampling events were performed spanning late spring/early summer (May) to late summer (September) in 2023, covering the period in which the GoA is characterized by oligotrophic N-poor conditions (Fuller et al., 2005; Mackey et al., 2007). Ancillary water column measurements included temperature, salinity, photosynthetic active radiation (PAR) (Seabird 19 Plus), inorganic nitrogen species concentrations (NO_2^-, NO_3^-, NH_4^+), chlorophyll-*a*, and rates of photosynthesis and dark inorganic carbon fixation (DCF).

2.1 Inorganic nitrogen species

Duplicate water samples for nitrite (NO_2^-) and nitrate (NO_3^-) were collected in 15 ml acid-clean polyethylene tubes directly from Niskin bottles. Prior to filling, the tube was thoroughly rinsed three times with sample water. After collection, samples were stored at 4 °C in the dark and analyzed the following day. Nitrite (NO_2^-) and nitrate (NO_3^-) concentrations were determined colorimetrically following standard procedures (Grasshoff et al., 1999). Nitrite was measured directly using the Griess reaction, in which nitrite forms an azo dye after reaction with sulfanilamide and N-(1-naphthyl)ethylenediamine and is quantified spectrophotometrically (λ=520 nm). Nitrate was reduced to nitrite using a copper-coated cadmium reduction column and subsequently nitrate + nitrite was analyzed by the same azo-dye method. Nitrate concentrations were then calculated by difference. Analyses were performed using a Flow Injection Autoanalyzer system (FIA, Lachat Instruments (Model QuikChem 8000). The analysis was automated, and peak areas were calibrated using standards prepared in nutrient-deplete 0.2-µm filtered surface seawater from the GoA over a range of 0-100 nmol L^{-1}. The detection limits were 10 nmol L^{-1} and 20 nmol L^{-1} for nitrite and nitrate, respectively, with typical analytical precision of ~20 nmol L^{-1}, consistent with previous measurements in the GoA (e.g., Mackey et al., 2011).

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Samples for ammonium (NH_4^+) concentration were collected directly from Niskin bottles into acid-washed plastic vials after rinsing 3 times with sample water. The collected samples were stored in 4 °C in the dark and analyzed within an hour after collection. Ammonium concentrations were determined using the orthophthaldialdehyde (OPA) method (Holmes et al., 1999), where samples were first incubated with a working reagent of OPA for 3 h and then measured fluorometrically (Turner Designs, Ex: 360 nm, Em. 420 nm). The detection limit of the OPA analysis was ~4 nmol L^{-1} (Meeder et al., 2012).

2.2 Ammonium and nitrite oxidation rates

Ammonium and nitrite oxidation rates were determined using stable isotope tracer incubations (Beman et al., 2011; Bristow et al., 2015; Ward, 1987). Seawater was collected into triplicate 0.5-L acid-cleaned transparent Nalgene bottles without headspace. The bottles were incubated on land for 24 h in aquarium tanks continuously supplied with running surface seawater, using neutral density screening nets simulating the light conditions of the collection depth (no change in spectra). For ammonia oxidation, samples were amended with ^{15}N-labeled ammonium chloride ($^{15}NH_4Cl$, >98 atom %; Cambridge Isotope Laboratories) at a concentration of ~20 nmol L^{-1} which was expected to provide a quantifiable signal without substantially enhancing oxidation rates. For nitrite oxidation, samples were amended with ~5 nmol L^{-1} of ^{15}N-labeled sodium nitrite ($^{15}NO_2^-$, >98 atom %), again minimally perturbing the *in situ* nitrite pool. At the end of the incubation, subsamples were filtered onto a Supor 0.22 µm (47 mm) filter using gentle filtration, and the filtrate (<0.22 µm) was kept frozen in the dark at -20 °C until analysis. For ammonia oxidation, the presence of $^{15}NO_2^-$ in the total dissolved nitrite pool was quantified by isotope ratio mass spectrometry (IRMS) after chemical conversion to N_2O using the azide method (McIlvin and Altabet, 2005). For nitrite oxidation, we quantified the $^{15}NO_3^-$ in the dissolved nitrate pool after conversion to nitrous oxide via the denitrifier method (Sigman et al., 2001) and subsequent IRMS analysis. Additionally, killed controls poisoned with $HgCl_2$ from each collection depth were incubated in parallel to account for any abiotic transformations and subtracted from the 'live' bottles. Rates in the 'mercury-killed' controls were typically negligible relative to the 'live' bottles. Rates of ammonium and nitrite oxidation were calculated following previous studies (Beman et al., 2011; Bristow et al., 2015; Ward, 1987) as shown in in Eq. 1-3:

$$(1)\ \text{Ammonia oxidation} = \frac{\Delta\ (\text{atm\% 15N NO2})\ \text{x}\ [\text{NO2}]\text{final}}{\text{t x F (NH4)}}$$

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(2) Nitrite oxidation $= \frac{\Delta\ (\text{atm\% 15N NO3}) \text{ x [NO3]final}}{\text{t x F (NO2)}}$

(3) F substrate $= \frac{[15N\ substrate]added}{\text{[Substrate ambient]+[Substrate added]}}$

Where, Δ(atm% $^{15}N\ NO_2^-$) or Δ(atm% $^{15}N\ NO_3^-$) = atom% excess ^{15}N in the nitrite or nitrate pool relative to natural abundance; $[NO_2^-]_{final}$ or $[NO_3^-]_{final}$ = final concentration of the nitrite or nitrate pool (nmol L^{-1}); t = time (d); F_{NH4} or F_{NO2} = fractional ^{15}N enrichment of the ammonium or nitrite substrate pool.

2.3 Photosynthesis and Dark Carbon Fixation (DCF)

Photosynthesis and chemoautotrophic DCF rates were measured using $NaH^{14}CO_3$ incorporation method (Steemann-Nielsen, 1952) with minor modifications (Reich et al., 2024, 2026). Triplicate seawater samples were collected from Niskin bottles in 50 ml acid-washed falcon tubes and spiked with a diluted 'working solution' of $NaH^{14}CO_3$ (Perkin Elmer, specific activity 56 mCi $mmol^{-1}$) at a final radioisotope dilution of $1{:}10^4$ *v:v.* Tubes were incubated in the same tanks and under the same conditions used for the ammonium and nitrite oxidation measurements with one exception – the DCF bottles were first covered with aluminum foil to prevent light penetration. The tubes were incubated for 24 h before being filtered onto GF/F filters (0.7 µm nominal pore size, 25 mm diameter) using low vacuum pressure (<50 mmHg). The filters were placed in glass scintillation vials and 50 µl of 37% hydrochloric acid was added to remove the non-fixed ^{14}C-bicarbonate overnight. Scintillation cocktail (5 ml, ULTIMA-GOLD) was then added to each vial and samples were counted using a TRI-CARB 4810 TR (Packard) liquid scintillation counter. Additional T_0 blanks were prepared by spiking bottles with $NaH^{14}CO_3$ and filtering immediately (without incubation). Blanks consistently yielded negligible activity. Added activity was measured by withdrawing 50 µl from representative spiked bottles (immediately after dosing and before incubation) and adding it onto a new GF/F filter with 50 µl of ethanolamine (pH≈12) followed by scintillation cocktail and counting immediately.

Photosynthesis was calculated as the difference between the disintegration per minute (DPM) measured in the samples incubated under ambient irradiance and the dark bottles. DCF and photosynthesis rates were calculated based on the Bermuda Atlantic Time-series Study (BATS) protocol using the following Eq. 4:

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(4) $Production = \frac{(DPM-blank)}{V} \times DIC \times \frac{AA\ vol}{TDPM} \times f \times \frac{1}{t}$

Where, DPM equals the disintegrations per minute, V = the filtered volume (50 ml), DIC is the dissolved inorganic carbon in seawater (~25 mg C L^{-1}, similar to other oceanic sites, (Knap and Michaels, 1993), AA vol = Added activity volume (50 µl), TDPM = Total ^{14}C disintegration per minute, t = incubation time (24h), and f = factor correcting isotope fractionation during uptake of ^{14}C (1.05).

2.4 Chlorophyll.*a* analysis

Seawater samples (250 ml) were filtered onto Whatman GF/F filters at low pressure (<150 mbar), placed in glass vials and frozen in the dark at -20 °C. Chlorophyll.*a* was extracted with 5 ml of cold acetone (90 %) overnight and determined by the non-acidification method (Welschmeyer, 1994) using a Turner Designs (Trilogy) fluorometer.

3 Results and discussion

3.1 Physiochemical and biological characteristics of the GoA during summertime

Sampling spanned from late spring (May) to the end of summer (September) within the euphotic zone (0-100 m) of the GoA. Surface temperatures ranged from ~25 °C in May to ~28 °C at the end of summer (September) and declined to ~23.5 °C at 100 m during all sampling events (Figure 1A). Photosynthetic active radiation (PAR) levels ranged from ~1200-1950 µmol quanta m^{-2} s^{-1} at the surface and decreased exponentially to ~10-20 µmol quanta m^{-2} s^{-1} at 100 m (Figure 1B), corresponding to 0.5-2% of the surface irradiation levels. The corresponding diffuse attenuation coefficient (Kd) was ~0.03-0.04 m^{-1}, in agreement with previous observations from the GoA (Dishon et al., 2012; Stambler, 2006) and other oligotrophic regimes (Stambler, 2012). Concentrations of NH_4^+ ranged from undetectable to 65 nmol L^{-1} without a clear vertical or temporal trend, except in May where surface concentrations were below detection (Figure 1C). The corresponding integrated NH_4^+ inventory (0-100 m) was lowest in May (1.68 µmol m^{-2}) and highest in July (~4.57 µmol m^{-2}) (Table 1). NO_2^- levels were generally low throughout the upper 100 m (from below detection to <20 nmol L^{-1}), except in September when nitrite increased with depth reaching ~45 nmol L^{-1} below 40 m (Figure 1D). Vertical NO_2^- profiles suggest active ammonia oxidation below the strongly lit surface waters, especially during September, although we cannot rule out expulsion of NO_2^- by phytoplankton under light limitation (Ko et al., 2022). Nevertheless, vertically

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integrated NO_2^- inventories were generally low in all months examined, ranging from 0.79-3.39 µmol m^{-2} (Table 1). Surface NO_3^- was also low (<20 nmol L^{-1}) and generally increased with depth, suggesting organic matter regeneration and nitrification during summertime (Figure 1E), and/or that less NO_3^- is assimilated by phytoplankton at deeper depths. The integrated NO_3^- inventory ranged from 2.65 µmol m^{-2} in May and September up to 10.36 µmol m^{-2} in June (Table 1). Taken together, the summertime inorganic N species concentrations in the upper 100 m were low, in agreement with previous reports from the oligotrophic GoA (Mackey et al., 2011; Meeder et al., 2012; Rahav et al., 2015). The general increasing trend in NO_2^- and NO_3^- with depth and the nano-molar NH_4^+ levels suggest active nitrification below the well-lit surface water that has not been previously quantified in the GoA.

Phytoplankton biomass derived from chlorophyll.*a* was low in the surface water (<0.15 µg L^{-1}) and gradually increased with depth reaching maximal values in May and June (~0.60 µg L^{-1}) (Figure 2A). The corresponding integrated chlorophyll.*a* was 26-28 mg m^{-2} except in August where it was 16 mg m^{-2} (Table 1). As expected, photosynthesis rates were highest in the surface water and decreased with depth (Figure 2B), coinciding with the decreasing PAR levels (Figure 1B). Photosynthesis rates decreased from ~10 µg C L^{-1} d^{-1} at the surface to below detection at 100 m, except in September when elevated rates were observed throughout the water column, ranging from ~10 to 25 µg C L^{-1} d^{-1} (Figure 2B). The resulting integrated photosynthesis rates ranged from 242 mg C m^{-2} d^{-1} in August to as high as 1263 mg C m^{-2} d^{-1} in September (Table 1). Despite the fluctuation in photosynthetic rates between months, these values are within the range previously reported from the GoA (Rahav et al., 2015; Reich et al., 2024; Suggett et al., 2009).

Chemoautotrophic DCF was lower than photosynthesis rates and exhibited no clear vertical trends (Figure 2C). The surface DCF ranged from ~0.2-0.6 µg C L^{-1} d^{-1} to ~0.1-0.9 µg C L^{-1} d^{-1} at 100 m (Figure 2C). The resulting integrated DCF ranged from 17-37 mg C m^{-2} d^{-1}, in agreement with a recent study from the GoA (Reich et al., 2024), corresponding to ~3-10% of all the total autotrophic activity (photosynthesis + DCF). While multiple microbial metabolisms involve chemoautotrophic carbon fixation, DCF is primarily attributed to ammonium and nitrite oxidation, as these chemoautotrophic metabolisms are ubiquitous throughout the oxic water column (Middelburg, 2011; Tang et al., 2023). In general, ammonia oxidation likely provides energy that supports chemoautotrophic CO_2 assimilation throughout the euphotic zone. Though less energy efficient, nitrite oxidation also contributes to DCF and is considered especially relevant near the base of the euphotic zone where NO_2^- often accumulates and reaches a maximum in concentration (Tang et al., 2023).

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229 **Table 1**: Summary of integrated values (0-100 m) measured in the GoA (N Red Sea) during
230 summer 2023.

Variable	May 23	June 23	July 23	Aug. 23	Sept. 23
NH_4^+ (µmol m^{-2})	1.68	4.54	4.57	3.36	2.99
NO_2^- (µmol m^{-2})	1.76	0.79	0.94	1.64	3.39
NO_3^- (µmol m^{-2})	2.76	10.36	6.60	6.13	2.65
Chlorophyll.*a* (mg m^{-2})	26	28	26	16	28
Photosynthesis (mg C m^{-2} d^{-1})	350	349	302	242	1263
DCF (mg C m^{-2} d^{-1})	32	17	35	27	37
NH_4^+ oxidation (µmol m^{-2} d^{-1})	28	48	39	45	56
NO_2^- oxidation (µmol m^{-2} d^{-1})	24	38	45	39	44
Contribution of NH_4^+ oxidation to DCF (%)*	0.32	1.02	0.40	0.60	0.54
Contribution of NO_2^- oxidation to DCF (%)**	0.05	0.13	0.08	0.09	0.07

231 *Assuming 0.3 moles of C fixed per mole of NH_4^+ oxidized (Santoro et al., 2010).

232 **Assuming 0.05 moles of C per mole of NO_2^- oxidized (Beman et al., 2013).
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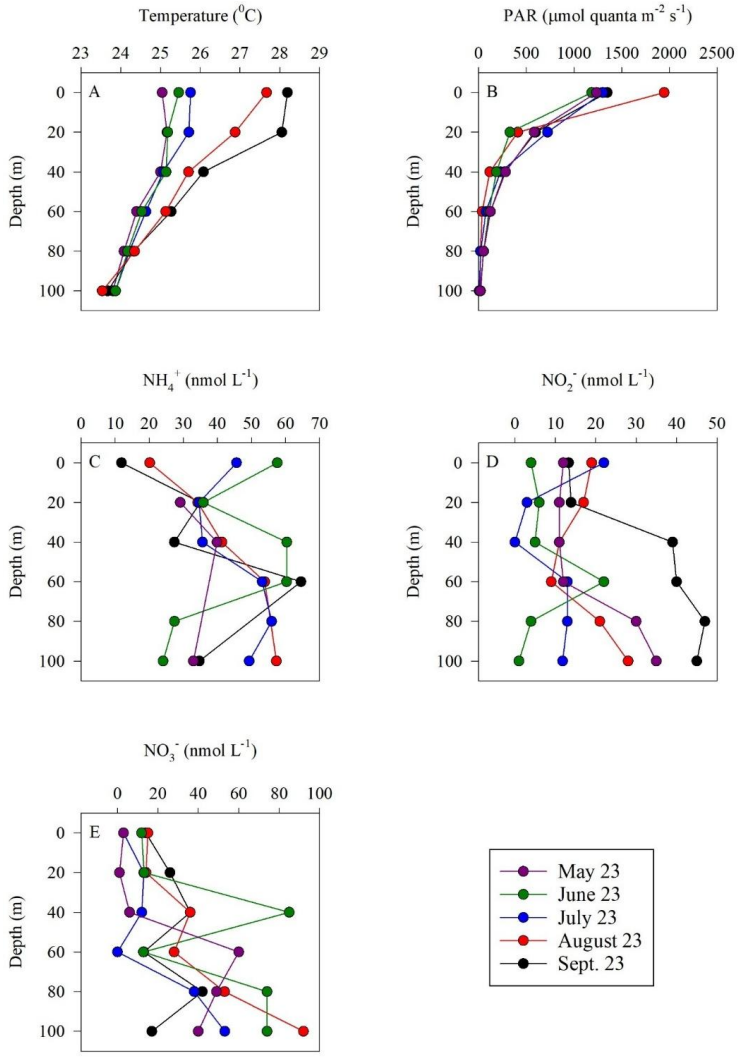

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235 **Figure 1**: Vertical distribution of temperature (A), PAR (B), NH_4^+ (C), NO_2^- (D) and NO_3^- (E)
236 in the upper euphotic zone in the GoA, N Red Sea between May and September 2023.

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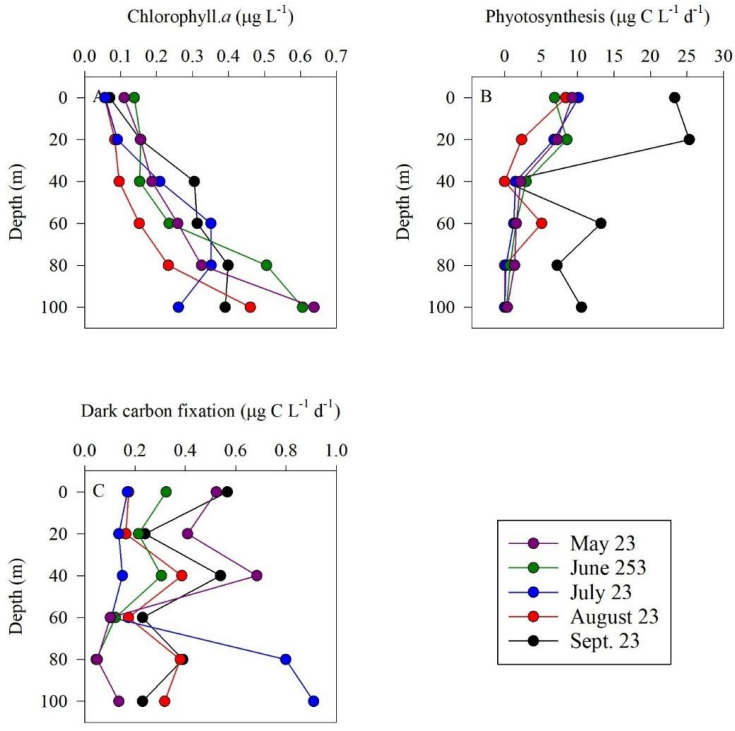

Figure 2: Vertical distribution of chlorophyll-a (A), photosynthesis (B), and dark carbon fixation (C) in the upper euphotic zone in the GoA, N Red Sea between May and September 2023.

3.2 Ammonia and nitrite oxidation rates

Ammonia and nitrite oxidation rates were generally low throughout the euphotic zone yet exhibited an increasing trend with depth (Figure 3), consistent with regulation by light inhibition. Overall, ammonia oxidation was homogeneous in the upper 40 m, ranging from ~0.10-0.55 nmol N L^{-1} d^{-1}. Below this depth rates increased towards the bottom of the euphotic zone (~100 m), ranging from ~0.26-0.83 nmol N L^{-1} d^{-1} (Figure 3A,B). Ammonia oxidation rates often reached a maximum near the base of the euphotic zone (below the 50-100 m layer) as seen in other studies (Tang et al., 2023). In general, these low euphotic zone ammonia oxidation rates are consistent with light inhibition, given the high PAR of the GoA during summer (Figure 1B, Wan et al., 2021). Competition of nitrifiers with phytoplankton for NH_4^+ may also result in low ammonia oxidation rates, as has been reported in the surface sunlit North Pacific (Smith et al., 2014). However, the highest integrated ammonia oxidation rate (September, 56 µmol m^{-2} d^{-1}) was measured when chlorophyll.*a* levels and primary

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productivity were also relatively high and similar to springtime when the lowest ammonia oxidation rates were measured (May, 28 μmol m^{-2} d^{-1}) (Table 1). Thus, competition between nitrifiers and phytoplankton for NH_4^+ does not appear to play a direct role in the regulation of oxidation rates in our study. This is further supported by the lack of correlation between chlorophyll.*a* and ammonium ($r^2 = 0.003$). Ammonia oxidation rates have also been shown to be influenced by trace metal availability, specifically iron and copper (Martocello and Wankel, 2024; Shafiee et al., 2019, 2021). However, given the close proximity to major deserts, iron is not considered a limiting factor for microbes in the surface water of the GoA (Chen et al., 2008; Torfstein et al., 2017). The limiting factors for ammonia oxidizers in the GoA should be further studied by simulating different nutrients and temperature scenarios with or without amendments of an inhibitor of ammonia monooxygenase to better examine controls on environmental rates (Bayer et al., 2024).

As with ammonia oxidation, rates of nitrite oxidation also increased with depth (Figure 3C,D). Nitrite oxidation ranged from 0.14 to 0.70 nmol L^{-1} d^{-1} (Figure 3C,D), with highest rates measured over 80-100 m. Integrated nitrite oxidation rates were lowest in spring/early summer (~24 μmol m^{-2} d^{-1}) and increased between June to September (38-45 μmol m^{-2} d^{-1}) (Table 1). Nitrite oxidation maxima (~100 m) were deeper than those of ammonia oxidation (~60 m), which may be related to the higher sensitivity of nitrite oxidizers to light (Wan et al., 2021). Our results demonstrate that ammonia and nitrite oxidation occurred at comparable rates, which is consistent with the typically low concentrations of NO_2^- observed in the GoA (Figure 1D, Meeder et al., 2012).

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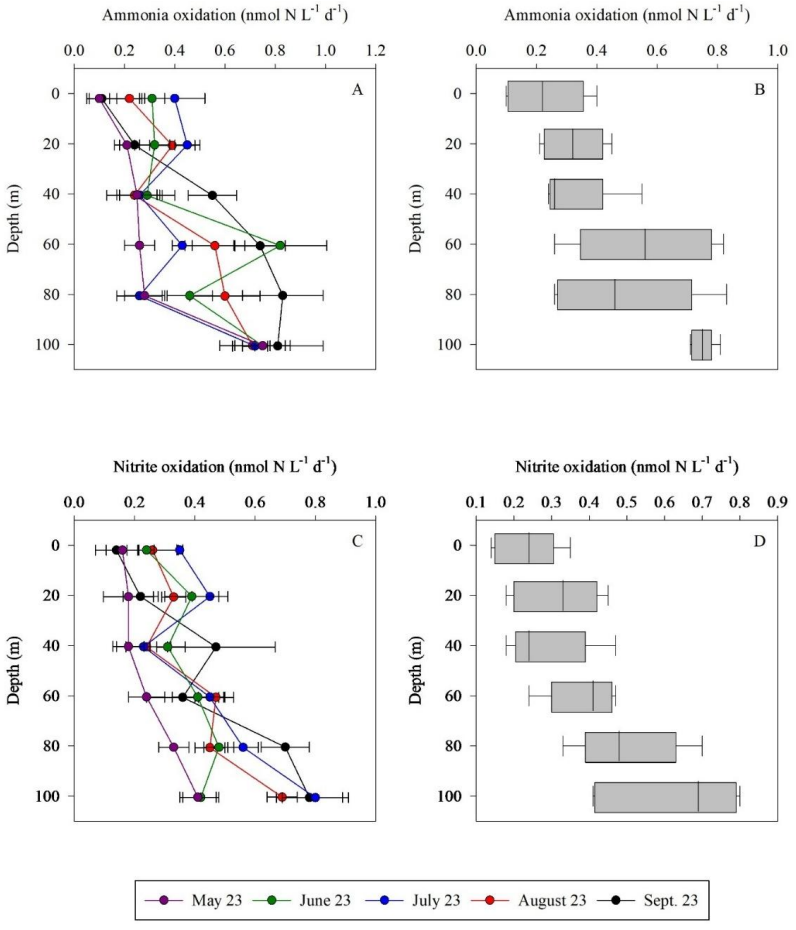

Figure 3: Vertical distribution of ammonia oxidation (A,B) and nitrite oxidation (C,D) in the upper euphotic zone in the GoA, N Red Sea between May and September 2023. The Box Wisker plots sum the data distribution per depth (n=5).

3.3 Contribution of ammonia and nitrite oxidation to DCF

DCF is widely thought to be dominated by ammonia and nitrite oxidation, as these metabolic processes provide energy that, in turn, support chemoautotrophic CO_2 assimilation (Middelburg, 2011). While other chemoautotrophic metabolisms, such as sulfur oxidation, anammox or methanotrophy also represent important drivers of chemoautotrophy in some environments, these are unlikely to be relevant in the oxic, oligotrophic waters of the GoA. DCF and nitrification are rarely measured simultaneously, which prevents robust assessment of this relationship. To this end, we explored DCF under the warm, high-light, nutrient-poor conditions found in the GoA (Figure 1) and how it relates to corresponding rates of nitrification

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over the euphotic zone. We calculated the contribution of ammonia and nitrite oxidation to DCF assuming 0.3 moles of C fixed per mole of NH_4^+ (Santoro et al., 2010). Overall, the depth-integrated contribution of ammonia oxidation to DCF ranged between 0-2%, consistent, yet often lower than reports from other oceanographic settings (Table 1). For example ammonia oxidizers contributed only a small fraction to DCF in the eastern tropical Pacific, accounting for <20% of depth-integrated rates (Bayer et al., 2024). The depth-integrated contribution of nitrite oxidation to DCF was negligible, accounting for 0.05-0.13%. (Table 1). Thus, ammonia and nitrite oxidation together could account for only ~1% of the DCF, lower than recent estimates from the eastern tropical Pacific (Bayer et al., 2024), though similar to observations in culture experiments with ammonia oxidizers (Bayer et al., 2023). It is notable, however, that relevant conversion factors between moles C fixed per mole of N oxidized in the ocean should be better constrained (and may be site-specific) (Tang et al., 2023), which could alter the calculated contribution discussed here. Nevertheless, we show that ammonia and nitrite oxidation link N recycling with inorganic carbon assimilation in the euphotic zone in the GoA, and while their contribution to total primary production is relatively small (e.g., Figure 2), it may sustain part of the microbial metabolism in the nutrient-depleted surface waters of the GoA. Our results also suggest that other microbial metabolism processes (e.g., anaplerosis) may also contribute to DCF in the GoA's euphotic zone and should be estimated separately in future studies.

3.4 Environmental divers affecting ammonium and nitrite oxidation

Nitrification is known to be affected by PAR, oxygen levels, temperature, nitrogen substrate availability, pH, as well as by other environmental factors (Ward, 2008). Our results are consistent overall with previous observations at other sites as both ammonium and nitrite oxidation rates linearly correlate with most of these environmental variables, either positively or negatively (Figure 4). Most notably, ammonium and nitrite oxidation rates correlated with increasing depth and decreasing PAR level, consistent with previous reports showing that light has generally been found to inhibit nitrifier growth and nitrification rates (Merbt et al., 2012; Olsen, 1989; Xu et al., 2019). Surprisingly, temperature correlated negatively with ammonium and nitrite oxidation rates (Figure 4). Previous studies showed that increasing temperature generally stimulates nitrification by simultaneously altering substrate availability and enzyme kinetics. As temperature increases, the pKa of the NH_4^+-NH_3 system decreases, shifting the equilibrium toward NH_3, the putative substrate of ammonia monooxygenase (Emerson et al., 1975). In parallel, warming enhances enzymatic activity, accelerating the catalytic steps of both

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ammonia and nitrite oxidation (Zheng et al., 2017, 2020). We surmise that in the stratified GoA, warming strengthened stratification, enhanced photoinhibition, and thereby increased biological competition for ammonium, thus reducing substrate supply to nitrifiers despite favorable enzyme kinetics, leading to the observed negative correlation between temperature and nitrification. In agreement with this line of thought, substrate availability was positively correlated with ammonia oxidation (NH_4^+, NO_2^-) and nitrite oxidation (NO_2^-, NO_3^-), highlighting the substrate-dependent nature of nitrification. Ammonia oxidation requires NH_4^+ or NH_3 as the electron donor, while nitrite oxidation depends on NO_2^- availability. Elevated ambient concentrations of these substrates make them more available to nitrifying enzymes, resulting in higher reaction rates until enzymatic saturation or co-limitation with other nutrients are reached (e.g., trace metal, PO_4^+). In oligotrophic systems such as the GoA, where ambient NH_4^+ and NO_2^- concentrations are exceptionally low, even small pulses of reduced or intermediate nitrogen (e.g., from organic matter remineralization, mixing, or atmospheric deposition) may trigger an increase in nitrification rates.

Nitrification is generally expected to show a negative relationship with chlorophyll.*a* in surface waters, where phytoplankton may compete with nitrifiers for reduced nitrogen species. Consequently, most studies report suppressed ammonium and nitrite oxidation rates near the surface and enhanced rates below the chlorophyll maximum once light levels decrease and substrate regeneration through organic matter remineralization becomes more important (Beman et al., 2013; Yool et al., 2007). Here, however, we observed a positive correlation between chlorophyll.*a* and ammonium or nitrite oxidation (as well as with photosynthesis, although not significantly). This trend can be explained by the deep setting of the chlorophyll maximum (~80-100 m), where phytoplankton biomass is relatively high, but light is low and organic matter turnover is high, potentially providing regenerated NH_4^+ that fuels nitrification. These findings suggest that the expected negative coupling at the surface is offset by strong regeneration and oxidation processes near the deep chlorophyll maxima, resulting in an overall positive relationship when integrated across the euphotic zone.

We expected that ammonium and nitrite oxidation would show a significant correlation with DCF (see discussion above). Nevertheless, although both ammonium and nitrite oxidation were positively coupled with DCF, the correlations were not statistically significant and is in line with the overall low contribution of these processes to DCF (discussion above and see Table 1). This suggests that additional pathways such as anaplerotic processes may contribute to DCF (Dijkhuizen and Harder, 1984; Erb, 2011), while the contribution of ammonium and nitrite oxidation to total DCF is low (Table 1).

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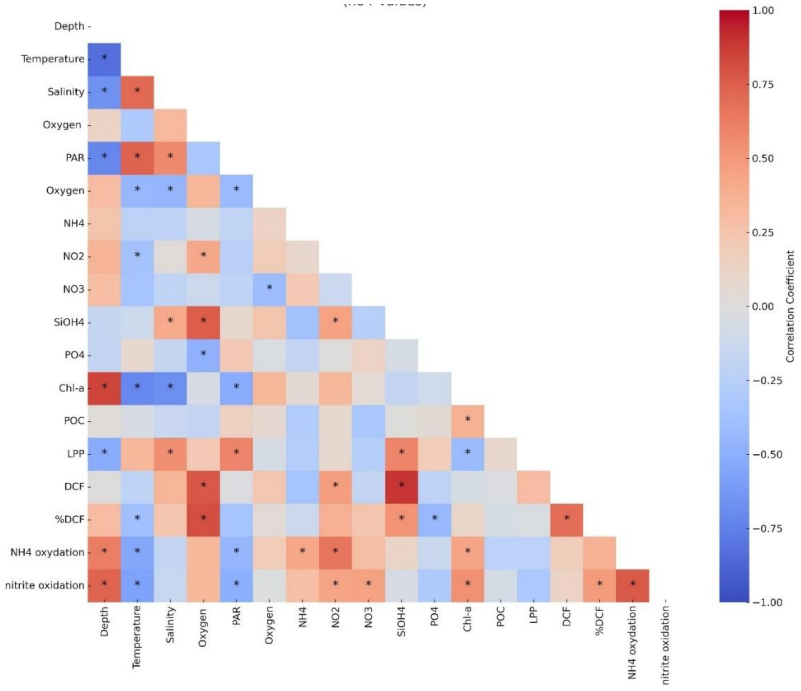

Figure 4: A heatmap showing Pearson correlation coefficients among measured environmental parameters and biogeochemical rates. Color shading indicates the strength and direction of the correlation. Asterisks denote statistically significant correlations ($p < 0.05$).

4 Conclusions

Globally, ammonium and nitrite oxidation rates in the euphotic zone span several orders of magnitude across oceanic environments (Figure 5). The rates we measured in the GoA during summer fall below these global medians (i.e., the red vs. black lines in Figure 5). The reason for the low rates in GoA is attributed to the low substrate availability during summertime (Figure 1C-E). The combination of high light intensity (Figure 1B) and penetration (i.e., Kd ≈ 0.04 m^{-1}) and enhanced stratification (Figure 1A) can further suppress nitrifier activity, either through photoinhibition of ammonia monooxygenase and/or by pushing microbial communities closer to their thermal tolerance limits. Our results emphasize that global compilations may be skewed toward more productive systems/seasons, and that nitrification in extremely nutrient-depleted regions may operate at lower rates and is tightly coupled to local nitrogen cycling.

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Future studies should focus on resolving the temporal and spatial variability of nitrification rates and nitrifier communities in the context of ongoing climate change. This is especially true for the GoA that experience rapid warming and ocean acidification. Long-term time series and diel-scale observations are needed to capture seasonal, interannual, and daily dynamics, particularly in relation to stratification, warming, and nutrient supply. Advanced molecular approaches such as metagenomics, metatranscriptomics, and single-cell tools should be applied to link community composition and functional potential with *in-situ* rate measurements. Parallel measurements of trace metals will be essential to assess their role as cofactors or inhibitors of key enzymes in ammonium and nitrite oxidation. Ultimately, combining high-resolution field observations with targeted manipulations and modelling will improve our ability to predict how nitrification responds to environmental change and contributes to current and future ocean nitrogen cycling.

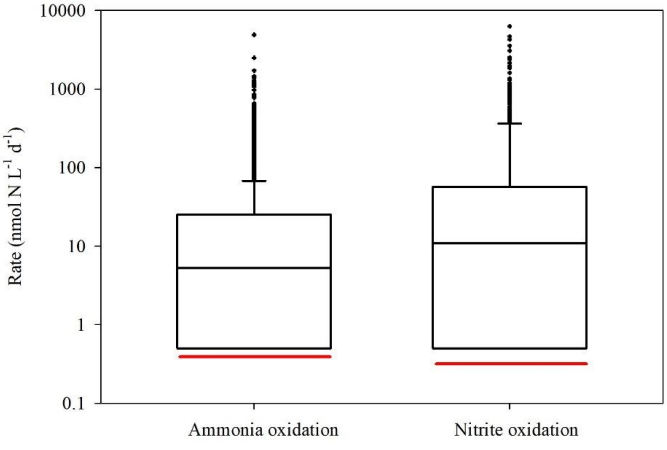

Figure 5: A literature compilation of reported euphotic zone's ammonia oxidation and nitrite oxidation recently reviewed Tang et al., (2023) and this study. The black line inside the boxes shows the median value of all studies considered, while the red line indicates the median values measured in the GoA during this study.

Data availability. All the data is presented in the graphs/table/text and will be made available in excel format upon request.

Author contributions. Conceptualized and conducted the field measurements; ER. Data curation, formal analysis, and visualization; ER, SDW and AP. The paper was prepared by ER, SDW and AP.

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Competing interests. The contact author has declared that none of the authors has any competing interests.

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References

Ali, M., Balala, A. C., Kumar, S., Bhavya, P. S., and Wafar, M.: Primary production in the northern Red Sea, J. Mar. Syst., 132, 75–82, https://doi.org/10.1016/j.jmarsys.2014.01.006, 2014.

Badran, M. I., Rasheed, M., Manasrah, R., Al-najjar, T., Station, M. S., and Faculty, V.: Nutrient flux fuels the summer primary productivity in the oligotrophic waters of the Gulf of Aqaba , Red Sea, Oceanologia, 47, 47–60, 2005.

Bayer, B., McBeain, K., Carlson, C. A., and Santoro, A. E.: Carbon content, carbon fixation yield and dissolved organic carbon release from diverse marine nitrifiers, Limnol. Oceanogr., 68, 84–96, https://doi.org/https://doi.org/10.1002/lno.12252, 2023.

Bayer, B., Kitzinger, K., Paul, N. L., Albers, J. B., Saito, M. A., Carlson, C. A., and Santoro, A. E.: Contribution of ammonia oxidizers to inorganic carbon fixation in the dark ocean, bioRxiv, https://doi.org/10.1101/2024.11.16.623942, 2024.

Bayer, B., Kitzinger, K., Paul, N. L., Albers, J. B., Saito, M. A., Wagner, M., Carlson, C. A., and Santoro, A. E.: Bayer 2025.pdf, Nat. Geosci, 18, 1144–1151, 2025.

Beman, J. M., Chow, C.-E., King, A. L., Feng, Y., Fuhrman, J. A., Andersson, A., Bates, N. R., Popp, B. N., and Hutchins, D. A.: Global declines in oceanic nitrification rates as a consequence of ocean acidification, Proc. Natl. Acad. Sci., 108, 208–213, https://doi.org/10.1073/pnas.1011053108, 2011.

Beman, J. M., Leilei Shih, J., and Popp, B. N.: Nitrite oxidation in the upper water column and oxygen minimum zone of the eastern tropical North Pacific Ocean, ISME J., 7, 2192–2205, https://doi.org/10.1038/ismej.2013.96, 2013.

Berman-Frank, I. and Rahav, E.: Nitrogen fixation as a source for new production in the Mediterranean Sea: a review, in: Life in the Mediterranean Sea: A Look at Habitat Changes, Nova Science Publishers, NY, 199–226, 2012.

Bristow, L. A., Sarode, N., Cartee, J., Caro-Quintero, A., Thamdrup, B., and Stewart, F. J.: Biogeochemical and metagenomic analysis of nitrite accumulation in the Gulf of Mexico hypoxic zone, Limnol. Oceanogr., 60, 1733–1750, https://doi.org/https://doi.org/10.1002/lno.10130, 2015.

Chen, Y., Paytan, A., Chase, Z., Measures, C., Beck, A. J., Sañudo-Wilhelmy, S. A., and Post, A. F.: Sources and fluxes of atmospheric trace elements to the Gulf of Aqaba, Red Sea, J. Geophys. Res. Atmos., 113, 1–13, https://doi.org/10.1029/2007JD009110, 2008.

Clark, D. R., Rees, A. P., and Joint, I.: Ammonium regeneration and nitrification rates in the oligotrophic Atlantic Ocean: Implications for new production estimates, Limnol. Oceanogr.,

https://doi.org/10.5194/egusphere-2026-855
Preprint. Discussion started: 6 March 2026

53, 52–62, https://doi.org/https://doi.org/10.4319/lo.2008.53.1.0052, 2008.

Clark, D. R., Rees, A. P., Ferrera, C. M., Al-moosawi, L., Somerfield, P. J., Harris, C., Quartly, G. D., Goult, S., Tarran, G., and Lessin, G.: Nitrite regeneration in the oligotrophic Atlantic Ocean, Biogeosciences, 19, 1355–1376, https://doi.org/https://doi.org/10.5194/bg-19-1355-2022, 2022.

Daims, H., Lebedeva, E. V, Pjevac, P., Han, P., Herbold, C., Albertsen, M., Jehmlich, N., Palatinszky, M., Vierheilig, J., Bulaev, A., Kirkegaard, R. H., von Bergen, M., Rattei, T., Bendinger, B., Nielsen, P. H., and Wagner, M.: Complete nitrification by Nitrospira bacteria, Nature, 528, 504–509, https://doi.org/10.1038/nature16461, 2015.

Dijkhuizen, L. and Harder, W.: Current views on the regulation of autotrophic carbon dioxide fixation via the Calvin cycle in bacteria, Antonie Van Leeuwenhoek, 50, 473–487, 1984.

Dishon, G., Dubinsky, Z., Caras, T., Rahav, E., Bar-Zeev, E., Tzubery, Y., and Iluz, D.: Optical habitats of ultraphytoplankton groups in the Gulf of Eilat (Aqaba), Northern Red Sea, Int. J. Remote Sens., 33, 2683–2705, https://doi.org/10.1080/01431161.2011.619209, 2012.

Emerson, K., Russo, R. C., Lund, R. E., and Thurston, R. V: Aqueous ammonia equilibrium calculations: effect of pH and temperature, J. Fish. Res. Board Canada, 32, 2379–2383, https://doi.org/10.1139/f75-274, 1975.

Eppley, R. W. and Peterson, B. J.: Particulate organic matter flux and planktonic new production in the deep ocean, Nature, 282, 677–680, https://doi.org/10.1038/282677a0, 1979.

Erb, T. J.: Carboxylases in natural and synthetic microbial pathways, https://doi.org/10.1128/AEM.05702-11, December 2011.

Fawcett, S. E., Lomas, M. W., Casey, J. R., Ward, B. B., and Sigman, D. M.: Assimilation of upwelled nitrate by small eukaryotes in the Sargasso Sea, Nat. Geosci., 4, 717–722, https://doi.org/10.1038/ngeo1265, 2011.

Fei, X., Jian-Gong, W., Ting, Z., Bin, Z., Sung-Keun, R., and Zhe-Xue, Q.: Ubiquity and diversity of complete ammonia oxidizers (Comammox), Appl. Environ. Microbiol., 84, e01390-18, https://doi.org/10.1128/AEM.01390-18, 2018.

Francis, C. A., Roberts, K. J., Beman, J. M., Santoro, A. E., and Oakley, B. B.: Ubiquity and diversity of ammonia-oxidizing archaea in water columns and sediments of the ocean, Proc. Natl. Acad. Sci., 102, 14683–14688, https://doi.org/10.1073/pnas.0506625102, 2005.

Fuller, N. J., West, N. J., Marie, D., Yallop, M., Rivlin, T., Post, A. F., Interuniversity, T., Sciences, M., Beach, C., and Scanlan, D. J.: Dynamics of community structure and phosphate status of picocyanobacterial populations in the Gulf of Aqaba , Red Sea, 50, 363–375, 2005.

Grasshoff, K., Kremling, K., and Ehrhardt, M.: Methods of seawater analysis, 3rd ed., edited by: Kremling, K., Ehrenreich, I. M., and Grasshoff, K., Wiley, New York, 632 pp., 1999.

Henriksen, K. and Kemp, W. M.: Nitrification in estuarine and coastal marine sediments, in: Nitrogen Cycling in Coastal Marine Environments, edited by: Blackburn, T. . and Sorensen, J., John Wiley & Sons, Ltd, 207–249, 1988.

Herbert, R. A.: Nitrogen cycling in coastal marine ecosystems, FEMS Microbiol. Rev., 23, 563–590, https://doi.org/10.1111/j.1574-6976.1999.tb00414.x, 1999.

Holms, R. ., Aminot, A., Kérouel, R., Hooker, B. ., and Peterson, B. .: A simple and precise

https://doi.org/10.5194/egusphere-2026-855
Preprint. Discussion started: 6 March 2026

method for measuring ammonium in marine and freshwater ecosystems, Can. Data Rep. Fish. Aquat. Sci., 56, 1801–1808, https://doi.org/10.1139/cjfas-56-10-1801, 1999.

van Kessel, M. A. H. J., Speth, D. R., Albertsen, M., Nielsen, P. H., Op den Camp, H. J. M., Kartal, B., Jetten, M. S. M., and Lücker, S.: Complete nitrification by a single microorganism, Nature, 528, 555–559, https://doi.org/10.1038/nature16459, 2015.

Ko, E., Gorbunov, M. Y., Jung, J., Lee, Y., Cho, K., Yang, E. J., and Park, J.: Phytoplankton photophysiology varies depending on nitrogen and light availability at the subsurface chlorophyll maximum in the northern Chukchi Sea, Front. Mar. Sci., 979998, https://doi.org/10.3389/fmars.2022.979998, 2022.

Mackey, K. R. M., Labiosa, R. G., Calhoun, M., Street, J. H., Post, A. F., and Paytan, A.: Phosphorus availability, phytoplankton community dynamics, and taxon-specific phosphorus status in the Gulf of Aqaba, Red Sea, Limnol. Oceanogr., 52, 873–885, https://doi.org/10.4319/lo.2007.52.2.0873, 2007.

Mackey, K. R. M., Bristow, L., Parks, D. R., Altabet, M. A., Post, A. F., and Paytan, A.: The influence of light on nitrogen cycling and the primary nitrite maximum in a seasonally stratified sea, Prog. Oceanogr., 91, 545–560, https://doi.org/https://doi.org/10.1016/j.pocean.2011.09.001, 2011.

Martocello, D. E. and Wankel, S. D.: Physiological influence of Fe and Cu availability on nitrogen isotope fractionation during ammonia oxidation, Environ. Sci. Technol., 58, 421–431, https://doi.org/10.1021/acs.est.3c05964, 2024.

McIlvin, M. R. and Altabet, M. A.: Chemical conversion of nitrate and nitrite to nitrous oxide for nitrogen and oxygen isotopic analysis in freshwater and seawater, Anal. Chem., 77, 5589–5595, https://doi.org/10.1021/ac050528s, 2005.

Mdutyana, M., Thomalla, S. J., Philibert, R., Ward, B. B., and Fawcett, S. E.: The seasonal cycle of nitrogen uptake and nitrification in the Atlantic sector of the Southern Ocean, Global Biogeochem. Cycles, 34, e2019GB006363, https://doi.org/https://doi.org/10.1029/2019GB006363, 2020.

Meeder, E., MacKey, K. R. M., Paytan, A., Shaked, Y., Iluz, D., Stambler, N., Rivlin, T., Post, A. F., and Lazar, B.: Nitrite dynamics in the open ocean-clues from seasonal and diurnal variations, Mar. Ecol. Prog. Ser., 453, 11–26, https://doi.org/10.3354/meps09525, 2012.

Merbt, S. N., Stahl, D. A., Casamayor, E. O., Martí, E., Nicol, G. W., and Prosser, J. I.: Differential photoinhibition of bacterial and archaeal ammonia oxidation, FEMS Microbiol. Lett., 327, 41–46, https://doi.org/10.1111/j.1574-6968.2011.02457.x, 2012.

Mescioglu, E., Rahav, E., Frada, M. J., Rosenfeld, S., Raveh, O., Galletti, Y., Santinelli, C., Herut, B., and Paytan, A.: Dust-associated airborne microbes affect primary and bacterial production rates, and eukaryotes diversity, in the Northern Red Sea: A mesocosm approach, Atmosphere (Basel)., 10, https://doi.org/10.3390/atmos10070358, 2019.

Middelburg, J. J.: Chemoautotrophy in the ocean, Geophys. Res. Lett., 38, 94–97, https://doi.org/10.1029/2011GL049725, 2011.

Mincer, T. J., Church, M. J., Taylor, L. T., Preston, C., Karl, D. M., and DeLong, E. F.: Quantitative distribution of presumptive archaeal and bacterial nitrifiers in Monterey Bay and the North Pacific Subtropical Gyre, Environ. Microbiol., 9, 1162–1175,

https://doi.org/10.5194/egusphere-2026-855
Preprint. Discussion started: 6 March 2026

https://doi.org/https://doi.org/10.1111/j.1462-2920.2007.01239.x, 2007.

Moutin, T. and Raimbault, P.: Primary production, carbon export and nutrients availability in western and eastern Mediterranean Sea in early summer 1996 (MINOS cruise), J. Mar. Syst., 33–34, 273–288, https://doi.org/10.1016/S0924-7963(02)00062-3, 2002.

Olsen, R.: Differential photoinhibition of marine nitrifying bacteria: a possible mechanism for the formation of the primary nitrite maximum, J. Mar. Syst., 31, 227–238, 1989.

Pachiadaki, M. G., Sintes, E., Bergauer, K., Brown, J. M., Record, N. R., Swan, B. K., Mathyer, M. E., Hallam, S. J., Lopez-Garcia, P., Takaki, Y., Nunoura, T., Woyke, T., Herndl, G. J., and Stepanauskas, R.: Major role of nitrite-oxidizing bacteria in dark ocean carbon fixation, Science (80-.)., 358, 1046–1051, https://doi.org/10.1126/science.aan8260, 2017.

Rahav, E., Herut, B., Mulholland, M. R., Belkin, N., Elifantz, H., and Berman-frank, I.: Heterotrophic and autotrophic contribution to dinitrogen fixation in the Gulf of Aqaba, Mar. Ecol. Prog. Ser., 522, 67–77, https://doi.org/10.3354/meps11143, 2015.

Reich, T., Belkin, N., Sisma-Ventura, G., Berman-Frank, I., and Rahav, E.: Significant dark inorganic carbon fixation in the euphotic zone of an oligotrophic sea, Limnol. Oceanogr., 9999, 1–14, https://doi.org/10.1002/lno.12560, 2024.

Reich, T., Belkin, N., Sisma-ventura, G., Hauzer, H., Berman-frank, I., and Rahav, E.: Does oligotrophy favor chemoautotrophy over photoautotrophy ?, Prog. Oceanogr., 241, 103633, https://doi.org/10.1016/j.pocean.2025.103633, 2026.

Santoro, A. E., Casciotti, K. L., and Francis, C. A.: Activity, abundance and diversity of nitrifying archaea and bacteria in the central California current, Environ. Microbiol., 12, 1989–2006, https://doi.org/https://doi.org/10.1111/j.1462-2920.2010.02205.x, 2010.

Shafiee, R. T., Snow, J. T., Zhang, Q., and Rickaby, R. E. M.: Iron requirements and uptake strategies of the globally abundant marine ammonia-oxidising archaeon, Nitrosopumilus maritimus SCM1, ISME J., 13, 2295–2305, https://doi.org/10.1038/s41396-019-0434-8, 2019.

Shafiee, R. T., Diver, P. J., Snow, J. T., Zhang, Q., and Rickaby, R. E. M.: Marine ammonia-oxidising archaea and bacteria occupy distinct iron and copper niches, ISME Commun., 1, 1, https://doi.org/10.1038/s43705-021-00001-7, 2021.

Shiozaki, T., Ijichi, M., Fujiwara, A., Makabe, A., Nishino, S., Yoshikawa, C., and Harada, N.: Factors regulating nitrification in the Arctic Ocean: potential impact of sea ice reduction and ocean acidification, Global Biogeochem. Cycles, 33, 1085–1099, https://doi.org/https://doi.org/10.1029/2018GB006068, 2019.

Sigman, D. M., Casciotti, K. L., Andreani, M., Barford, C., Galanter, M., and Böhlke, J. K.: A bacterial method for the nitrogen isotopic analysis of nitrate in seawater and freshwater, Anal. Chem., 73, 4145–4153, https://doi.org/10.1021/ac010088e, 2001.

Stambler, N.: Light and picophytoplankton in the Gulf of Eilat (Aqaba), J. Geophys. Res., 111, C11009, 2006.

Stambler, N.: Underwater light field of the Mediterranean Sea, in: Life in the Mediterranean Sea: A Look at Habitat Changes, edited by: Stambler, N., Nova Science Publishers, 1–739, 2012.

Steemann-Nielsen, E.: The use of radioactive carbon (14C) for measuring organic production

https://doi.org/10.5194/egusphere-2026-855
Preprint. Discussion started: 6 March 2026

in the sea, J. des Cons. Int. Pour Explor. la Mer, 18, 117–140, 1952.

Suggett, D. J., Stambler, N., Prášil, O., Kolber, Z., Quigg, A., VÃ□Â¡zquez-Dominguez, E., Zohary, T., Berman, T., Iluz, D., Levitan, O., Lawson, T., Meeder, E., Lazar, B., Bar-Zeev, E., Medova, H., and Berman-Frank, I.: Nitrogen and phosphorus limitation of oceanic microbial growth during spring in the Gulf of Aqaba, Aquat. Microb. Ecol., 56, 227–239, 2009.

Tang, W., Ward, B. B., Beman, M., Bristow, L., Clark, D., Fawcett, S., Frey, C., Fripiat, F., Herndl, G. J., Mdutyana, M., Paulot, F., Peng, X., Santoro, A. E., Shiozaki, T., Sintes, E., Stock, C., Sun, X., Wan, X. S., Xu, M. N., and Zhang, Y.: Database of nitrification and nitrifiers in the global ocean, Earth Sci. Rev., 15, 5039–5077, https://doi.org/https://doi.org/10.5194/essd-15-5039-2023, 2023.

Torfstein, A., Teutsch, N., Tirosh, O., Shaked, Y., Rivlin, T., Zipori, A., Stein, M., Lazar, B., and Erel, Y.: Chemical characterization of atmospheric dust from a weekly time series in the north Red Sea between 2006 and 2010, Geochim. Cosmochim. Acta, 211, 373–393, https://doi.org/10.1016/j.gca.2017.06.007, 2017.

Wan, X. S., Sheng, H.-X., Dai, M., Church, M. J., Zou, W., Li, X., Hutchins, D. A., Ward, B. B., and Kao, S.-J.: Phytoplankton-nitrifier interactions control the geographic distribution of nitrite in the upper ocean, Global Biogeochem. Cycles, 35, e2021GB007072, https://doi.org/https://doi.org/10.1029/2021GB007072, 2021.

Wankel, S. D., Kendall, C., Pennington, J. T., Chavez, F. P., and Paytan, A.: Nitrification in the euphotic zone as evidenced by nitrate dual isotopic composition: Observations from Monterey Bay , California, Glob. Biochem. cycles, 21, 1–13, https://doi.org/10.1029/2006GB002723, 2007.

Ward, B. B.: Nitrogen transformations in the Southern California Bight, Deep Sea Res. Part A. Oceanogr. Res. Pap., 34, 785–805, https://doi.org/https://doi.org/10.1016/0198-0149(87)90037-9, 1987.

Ward, B. B.: Nitrification in Marine Systems, in: Nitrogen in the Marine Environment Environment, edited by: Capon, D. G., Bronk, D. A., Mulholland, M. R., and Carpenterl, E. J., Elsevier, 199–262, https://doi.org/10.1016/B978-0-12-372522-6.00005-0, 2008.

Welschmeyer, N. A.: Fluorometric analysis of chlorophyll a in the presence of chlorophyll b and pheopigments, Limnol. Oceanogr., 39, 1985–1992, 1994.

Wuchter, C., Abbas, B., Coolen, M. J. L., Herfort, L., van Bleijswijk, J., Timmers, P., Strous, M., Teira, E., Herndl, G. J., Middelburg, J. J., Schouten, S., and Sinninghe Damsté, J. S.: Archaeal nitrification in the ocean, Proc. Natl. Acad. Sci., 103, 12317–12322, https://doi.org/10.1073/pnas.0600756103, 2006.

Xu, M. N., Li, X., Shi, D., Zhang, Y., Dai, M., Huang, T., Glibert, P. M., and Kao, S.-J.: Coupled effect of substrate and light on assimilation and oxidation of regenerated nitrogen in the euphotic ocean, Limnol. Oceanogr., 64, 1270–1283, https://doi.org/https://doi.org/10.1002/lno.11114, 2019.

Yool, A., Martin, A. P., Fernández, C., and Clark, D. R.: The significance of nitrification for oceanic new production, Nature, 447, 999–1002, https://doi.org/10.1038/nature05885, 2007.

Zheng, Z.-Z., Wan, X., Xu, M. N., Hsiao, S. S.-Y., Zhang, Y., Zheng, L.-W., Wu, Y., Zou, W., and Kao, S.-J.: Effects of temperature and particles on nitrification in a eutrophic coastal

https://doi.org/10.5194/egusphere-2026-855
Preprint. Discussion started: 6 March 2026

bay in southern China, J. Geophys. Res. Biogeosciences, 122, 2325–2337, https://doi.org/https://doi.org/10.1002/2017JG003871, 2017.

Zheng, Z.-Z., Zheng, L.-W., Xu, M. N., Tan, E., Hutchins, D. A., Deng, W., Zhang, Y., Shi, D., Dai, M., and Kao, S.-J.: Substrate regulation leads to differential responses of microbial ammonia-oxidizing communities to ocean warming, Nat. Commun., 11, 3511, https://doi.org/10.1038/s41467-020-17366-3, 2020.

Zhu, W., Wang, C., Hill, J., He, Y., Tao, B., Mao, Z., and Wu, W.: A missing link in the estuarine nitrogen cycle? Coupled nitrification-denitrification mediated by suspended particulate matter, Sci. Rep., 8, 2282, https://doi.org/10.1038/s41598-018-20688-4, 2018.