

Sinking particle fluxes and nitrogen loss in the eastern tropical North Pacific oxygen deficient zone measured using incubating sediment traps

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Abstract

Drifting sediment traps capable of *in situ* experimentation were deployed in the eastern tropical North Pacific (ETNP) within the world's largest oxygen deficient zone (ODZ; oxygen < 10 nM) over three cruises (January 2017, April 2018, and October 2019). This high-resolution sediment trap dataset does not follow a Martin curve. We consistently observe an 'inverted flux' wherein fresh organic matter was injected into the ODZ itself, originating *in situ* at the secondary chlorophyll maximum (SCM) from ODZ-dwelling cyanobacteria, and deeper (200–400 m) by additions from vertically migrating zooplankton. *In situ* labeling experiments to quantify total N₂ production rates, the first of their kind, are larger than previous ship-board incubations. *In situ* N₂ production rates distinguish between particle-associated production and production from the dissolved component of the water column, and suggest that except at the SCM, nitrogen gas production is dominated by sinking particles. Estimates of nitrogen loss over the entire ETNP (24.0 Tg N y⁻¹ for sinking particles and 40.7 Tg N y⁻¹ for water column and sinking particles combined) roughly agree with earlier estimates based on the nitrogen deficit approach.

Introduction

Oxygen deficient zones (ODZs) occur where aerobic respiration of organic matter combines with water column stabilization to form a persistent, low-oxygen layer at mid-depths. While ODZs make up less than 1% of global ocean volume, they account for 30–50% of oceanic nitrogen loss as N₂ (DeVries et al., 2013; Paulmier & Ruiz-Pino, 2009). This loss of bioavailable nitrogen from marine waters drives nitrogen limitation of primary productivity over vast regions of the ocean (Deutsch et al., 2004), making ODZs disproportionately important regions for marine fertility, foodwebs, and carbon cycling. The eastern tropical North Pacific (ETNP) hosts the Earth's largest ODZ (Paulmier & Ruiz-Pino, 2009), where the flux of organic carbon from the surface to the deep both fuels and responds to anoxic conditions, leading to a well-documented enhanced transfer efficiency of organic matter through the ODZ (Cram et al., 2022; Devol & Hartnett, 2001; Keil et al., 2016; Van Mooy et al., 2002). This enhanced transfer efficiency is likely due to the resistance to degradation of a fraction of the sinking particulate organic matter (POM) under anoxic conditions (Van Mooy et al., 2002). Additionally, since swimming zooplankton fragment and consume particles (Dilling & Alldredge, 2000; Goldthwait et al., 2004; Møller & Riisgård, 2007), the reduced respiration and activity of zooplankton that migrate into the ODZ (Kiko et al., 2015, 2016; Seibel et al., 2016) may also play a role in the enhanced transfer efficiency found there (Cram et al., 2022; Keil et al., 2016; Weber & Bianchi, 2020). Recently, particle production has been found in the ETNP ODZ at the depth of vertical migration of zooplankton and forage fish in the core of the ODZ (Cram et al., 2022; Fuchsman et al., 2025; Fuchsman & Cram, 2025) and at a secondary chlorophyll maximum (SCM) at the top of the ODZ, due to photosynthesis of ODZ specific *Prochlorococcus* (Fuchsman, Palevsky, et al., 2019; Fuchsman & Cram, 2025; Garcia-Robledo et al., 2017).

N₂ gas production in ODZs is inextricably linked to POM because the metabolisms responsible for N₂ production, mainly heterotrophic denitrification and autotrophic anammox, both rely directly (Babbin et

al., 2014; Chang et al., 2014) or indirectly on organic matter (Devol, 2003; Ganesh et al., 2015; Karthäuser et al., 2021). N_2 production has been shown to occur in particles in hypoxic waters in the lab (Stief et al., 2016); in the field (Fuchsman, Paul, et al., 2019); and in models, where > 50% of oceanic water column N_2 gas production was predicted to occur in sinking particles in hypoxic waters (Bianchi et al., 2018). Microbiology indicates that denitrification genes are enhanced on particles and anammox genes are enhanced in the water column in ODZs (Fuchsman et al., 2012, 2017; Ganesh et al., 2014). However, the partitioning of N_2 production rates between sinking particles and the water column in ODZs has never been examined.

Despite the linkages between nitrogen loss processes and organic matter, little is known of the heterogeneity with depth and time in ODZ systems, particularly with regard to sinking POM and its oxidation to inorganic carbon and N_2 gas (Fuchsman et al., 2025). In general, most of what has been learned about sinking particle dynamics has come from long-term sediment trap deployments (Church et al., 2013; Thunell et al., 2000) and lab experiments, including work under low oxygen (Ploug & Bergkvist, 2015; Stief et al., 2016). High-resolution, seasonal, short-timeframe sediment trap deployments may provide invaluable additional information on sinking POM and help to fill this knowledge gap. Compared to export estimates based on thorium isotope tracers or Underwater Vision Profilers (UVPs), which offer broad spatial and temporal coverage (Coale & Bruland, 1985; Cram et al., 2022; Henson et al., 2011; Pavia et al., 2019; Roullier et al., 2014), unpoisoned, high-resolution sediment traps have the advantage of collecting discrete samples of sinking particles that can be directly evaluated for microbial and geochemical properties. Traps with sizable collection areas, such as those used here, are particularly valuable for gathering large amounts of material (Keil et al., 2016; Peterson et al., 2005), a critical advantage in oligotrophic regions like the ETNP, while additionally allowing for downstream analyses such as rate incubations (Babbin et al., 2014; Raven et al., 2021; Van Mooy et al., 2002) or combined proteomics and genomics (Duffy et al., 2022; Fuchsman, Palevsky, et al., 2019). Their advantage over analyses of POM collected from water samples (Close et al., 2014; Fuchsman & Cram, 2025; Wakeham & Canuel, 1988), is that the material in sediment traps is confirmed to be sinking material.

As the main mechanism of organic flux from surface to depth (Nowicki et al., 2022), sinking particles are highly desirable for experiments estimating production and metabolic rates in the ocean's twilight zone. However, such measurements are challenging because bringing seawater, POM, and microorganisms to the surface disrupts *in situ* conditions of oxygen, pressure, and temperature conditions especially difficult to replicate for hypoxic and anoxic systems like the ETNP ODZ. In typical shipboard incubations measuring N_2 production, anoxic seawater collected with CTD Niskin bottles or pump systems can be rapidly contaminated with oxygen (Garcia-Robledo et al., 2021). Additionally, particle collection from Niskin bottles is hampered by gravitational settling: particles larger than $\sim 16 \mu m$ sink below the sampling port and are thus often lost during sampling collection (Fuchsman & Cram, 2025; Gardner, 1977; Suter et al., 2017).

In this work, we address both the unknown link between POM and N₂ dynamics and the methodological challenge of studying N₂ production rates deep within an ODZ. To better understand carbon and nitrogen dynamics in the ETNP ODZ, we couple highly depth-resolved sinking fluxes measured over three different seasons with *in situ* N₂ production measurements (Fig. 1), the first of their kind, providing a link between the supply of POM and the loss of bioavailable nitrogen and illuminating the partitioning of N₂ production between particles and the water column in ODZs.

Results

Hydrography

Three stations were examined over three cruises with St P2 and St P1 examined in January 2017 and April 2018 and St P2 and St P3 examined in October 2019. The depths of both the top and bottom of the ODZ varied among stations. The ODZ had a sharp upper oxycline at the slope St P1 (60 m), offshore St P2 (100 m), and northern offshore St P3 (160 m), and a deeper oxycline at ~ 850–1000 m at St P1 and P2 and 660–1000 m at St P3, where measurable oxygen returned (Fig. 2; Fig S1). Thus, St P1 had the thickest ODZ and St P3 had the thinnest. We define the ODZ as the zone where oxygen was generally below the SeaBird SBE 43 sensor detection limits ($< 1 \mu\text{mol kg}^{-1}$). Nitrite concentrations were elevated at all stations examined (Fig S2; see also Fuchsman et al., 2025 and Fuchsman & Cram, 2025), which is confirmation of anoxia (Banse et al., 2017). The euphotic zone mixed layer depths varied ± 5 m between casts at the same station (Fig S3).

Net primary production

To put our sinking flux data into context, we examined net primary productivity (NPP) determined from MODIS satellite observations during our three-year sampling period. The satellite-based estimates of NPP show high seasonality at slope St P1 and northern offshore St P3, with high productivity in the spring and the lowest productivity in the fall/early winter, but little seasonality at the more oligotrophic offshore St P2 (Fig. 2). Station P2, which we visited for approximately weeklong periods in January 2017, April 2018, and October 2019, was oligotrophic with no evident strong seasonality, with the 8-day average NPP for each visit of 51, 41, and 36 mmol C m⁻² day⁻¹, respectively (Fig. 2). In October 2019, NPP for St P2 was the lowest seen in the 3-year period (Fig. 2). During our sampling at St P1 in January 2017, the 8-day NPP was quite low at 37 mmol C m⁻² day⁻¹, similar to, or lower than, levels at St P2, and much lower than found during our April 2018 expedition (71 mmol C m⁻² day⁻¹). The spring maxima timing and magnitude at St P1 varied over the three years of our study. At St P1, the NPP maximum in spring of 2017 (May; 83 mmol C m⁻² day⁻¹) was similar to maxima in spring of 2018 in both March and May (89 then 87 mmol C m⁻² day⁻¹), but during the following spring of 2019, the NPP maxima was lower at 51–58 mmol C m⁻² day⁻¹ over the same March-May period (Fig. 2). At the northern offshore St P3, production was also seasonal with spring maxima in June, later in the year than the more southern St

P1. Spring maxima varied between years, with the highest NPP observed in June 2017 ($78 \text{ mmol C m}^{-2} \text{ day}^{-1}$) compared with June 2018 or 2019 (59 and 56 $\text{mmol C m}^{-2} \text{ day}^{-1}$, respectively). During our sampling at St P3 in October 2019, the 8-day average NPP was $45 \text{ mmol C m}^{-2} \text{ day}^{-1}$, the minimum for the year (Fig. 2). Thus, October 2019 was a particularly low productivity period.

Below the mixed layer (Fig S3), both St P1 and P2 consistently exhibited depth profiles with a primary “deep” chlorophyll maximum (DCM) in the sub-surface and a secondary chlorophyll-a maximum (SCM) in the ODZ (Fig. 2b-c). Northern offshore St P3 had a DCM but no SCM (Fig. 2d). Previous data from April 2012 indicated equivalent primary production rates in the mixed layer and at the DCM at St P2 and P1 (Fuchsman, Palevsky, et al., 2019). Therefore, there was likely an extended vertical region of primary productivity at these stations. Primary production at the SCM has been found to be substantially lower than at the DCM at stations not far from our slope St P1 and offshore P2 in May–June 2014 (Garcia-Robledo et al., 2017).

Sinking particle fluxes

Sediment trap sinking particle flux measurements were deployed primarily within the upper- and mid-ODZ, though trapping was also targeted at the base of the lower oxycline. Organic carbon and total nitrogen fluxes showed similar attenuation with depth at all three stations (Fig. 3). At slope St P1, despite the higher NPP in 2018, organic carbon sinking flux rates were lower in April 2018 ($244 \mu\text{mol C m}^{-2} \text{ day}^{-1}$ at 50 m) than in January 2017 ($477 \mu\text{mol C m}^{-2} \text{ day}^{-1}$ at 68 m). In the upper ODZ, fluxes were consistent between cruises at St P1 at $\sim 50 \mu\text{mol C m}^{-2} \text{ day}^{-1}$, but in 2017 larger fluxes ($\sim 100 \mu\text{mol C m}^{-2} \text{ day}^{-1}$) were sporadically seen. Higher fluxes ($\sim 100\text{--}200 \mu\text{mol C m}^{-2} \text{ day}^{-1}$) were measured between 200–400 m than were found in the upper ODZ. In January 2017 and April 2018, flux profiles at St P2 were largely similar and ranged from $114\text{--}185 \mu\text{mol C m}^{-2} \text{ day}^{-1}$ at 100 m to $12 \mu\text{mol C m}^{-2} \text{ day}^{-1}$ at 965 m. In the upper ODZ, sinking fluxes were consistent between 2017 and 2018 cruises at $\sim 100 \mu\text{mol C m}^{-2} \text{ day}^{-1}$. At this station, the highest fluxes were found around the secondary chlorophyll maximum (Fig. 3). Fluxes were lowest during October 2019 when we occupied both St P2 and northern offshore station P3. At St P2 in 2019, with the exception of a shallow deployment at 90 m that had a flux of $353 \mu\text{mol C m}^{-2} \text{ day}^{-1}$, fluxes rapidly attenuated to $16\text{--}24 \mu\text{mol C m}^{-2} \text{ day}^{-1}$ in the upper ODZ, but had a single increased flux measurement at 520 m ($86 \mu\text{mol C m}^{-2} \text{ day}^{-1}$). At St P3, fluxes ranged from $39 \mu\text{mol C m}^{-2} \text{ day}^{-1}$ at 102 m to $17 \mu\text{mol C m}^{-2} \text{ day}^{-1}$ at 965 m.

Despite large changes in satellite-derived NPP, especially at St P1 (Fig. 2), sinking fluxes were consistent across time and between stations (Fig. 3). There are two issues with a presumed linkage between satellite NPP and sinking fluxes in this system. First, satellite-derived NPP is based on remote sensor observations of the surface ocean, but in the offshore ETNP, maximal phytoplankton biomass is often found at the DCM (Fig. 4 and Garcia-Robledo et al., 2017) with extensive euphotic zone area below the mixed layer. Secondly, the fraction of primary productivity that is exported versus recycled via grazing

and the microbial loop (e value) can vary, though large variations are more typical in higher latitudes (Laurenceau-Cornec et al., 2023). Calculated e values (Fig. 4) indicate efficient recycling in the euphotic zone. In 2017 and 2019 organic matter flux at 100 m had a significant correlation with satellite NPP (Fig S4; $R^2 = 0.98$ $p = 0.008$). However, when data from St P1 in 2018 was included, the correlation became insignificant (Fig S4; $R^2 = 0.03$ $p = 0.7$). At St P1 in 2018, the highest chlorophyll was detected at the surface instead of at a DCM and the mixed layer was $\sim 5\text{--}10$ m (Fig S3). Thus, the satellite productivity measurement measured a small volume of water and was not necessarily representative of the euphotic zone as a whole. In estuaries where biomass and rates of primary productivity are decoupled, sinking fluxes are linked to the biomass of primary producers rather than primary productivity rates (Malone et al., 1996). To better link to sinking flux, similarly to Malone et al. (1996) we examined the biomass in the euphotic zone, both in and below the mixed layer, using chlorophyll measurements and concentrations of suspended organic C (Fig. 4). Both biomass-type measurements show high similarity between years and stations (Fig. 4). At St P2, suspended organic C concentrations were low in the surface ($\sim 3 \mu\text{M}$), but highest at the DCM ($5\text{--}6 \mu\text{M}$) at ~ 50 m. Biomass measurements were similar at St P2, even in October 2019 when primary production was particularly low. At St P3, suspended organic C was similar at the surface and DCM at $\sim 5 \mu\text{M}$ org C. At slope St P1, biomass was highest in the upper euphotic zone. St P1 had a thin high biomass maximum ($20 \mu\text{M}$ org C at 20 m) in 2017, but which decreased to $3 \mu\text{M}$ org C by 30 m depth. While satellite-derived surface NPP was highest at St P1 in 2018 ($71 \text{ mmol C m}^{-2} \text{ day}^{-1}$), biomass was $\sim 5 \mu\text{M}$ org C at 20 m. However, the highest chlorophyll at this station and time was at the surface (Fig S1), where biomass was not measured. There is a significant correlation between sinking flux at 100 m and maximal suspended POM concentrations even when including St P1 from 2018 (Fig S4; $R^2 = 0.66$, $p = 0.09$). We originally hypothesized that the more coastal slope station (~ 50 km from shore with 2200 m water depth) would have higher sinking fluxes than the offshore station. The consistent measurements of the biomass of primary producers across stations and time make the consistent sinking particle fluxes more understandable.

To varying degrees, all sediment trap profiles at the three stations had increases in sinking particle fluxes beneath the top of the ODZ, between 200 and 400 m depth (Fig. 3). As a comparison to other studies, we fit a power law function (Martin et al., 1987) also using 100 m reference depth z_0 to compare vertical sinking organic carbon attenuation at each station (Fig. 5). As anticipated, fits to a power law were poor, reflecting the non-Martin like flux profiles we consistently observed. Combining flux measurements from 2017 and 2018, slope St P1 had an attenuation coefficient (b) of 0.23 and with a poor fit ($R^2 = 0.05$). The attenuation coefficient at St P2 for combined 2017, 2018, and 2019 was 0.52 ($R^2 = 0.18$). At St P3, the attenuation coefficient was 0.45 ($R^2 = 0.41$) (Fig. 5). Combining all stations' flux measurements from all three years, the overall ETNP ODZ station attenuation coefficient was 0.48 ($R^2 = 0.18$) (Fig. 5); as seen in other studies, flux attenuation was lower than for more oxygenated regions of the ocean (Cram et al., 2022; Devol & Hartnett, 2001; Keil et al., 2016; Martin et al., 1987; Thunell et al., 2000; Van Mooy et al., 2002; Weber & Bianchi, 2020).

In situ N₂ production rates

Rates of N₂ production were measured in both January 2017 and April 2018 at the central offshore St P2 and slope St P1 (Fig. 6, Table S1). Slope station P1 had consistently higher N₂ production rates than offshore St P2. No successful rate measurements were made for the October 2019 expedition to Stations P2 and P3 due to sample loss. Raw N₂ production rates from the +particles chambers (Fig S5) were adjusted to represent N₂ production solely due to sinking particles in the water column. The rates from the water column chambers thus represent overall N₂ production in the water column, including both sinking and suspended particles, while the difference between the adjusted +particles chamber rates and water column rates represent N₂ production from suspended and/or dissolved sources.

Rates of overall water column N₂ production derived from the water column chamber *in situ* incubations, which included the particles found in that water, were variable, but on average across the entire dataset, were either the same or slightly greater than the particle N₂ production rates, indicating that sinking particles are important contributors to the overall N₂ production rate within the water column (Fig. 6). The notable exception is at the offshore Station P2 in April 2018, where sinking particle N₂ production rates exceeded or equaled overall water column rates (Fig. 6D) (see discussion of this station below). At the slope St P1 in 2017 and 2018, overall water column and sinking particle N₂ production rates had generally decreasing trends, though the highest overall water column rates, 18 and 50 nM N day⁻¹, 2017 and 2018, respectively, were beneath the SCM ~ 130–150 m depth and these corresponded to relatively lower sinking particle N₂ production rates (Fig. 6A, B). Rates of N₂ production from sinking particles in the offshore Station P2 ODZ ranged between 0.79–7.90 nM N day⁻¹ in January 2017 and 0.70–21.09 nM N day⁻¹ in April 2018. The notably higher rates in April 2018 did not correspond to overall higher sinking particle fluxes (Fig. 3, Fig. 6). In January 2017 at St P2, sinking particle N₂ production rates decreased with depth in the ODZ within the 100 to 180 m range sampled (Fig. 6C). In April 2018 at St P2, we had more successful incubations deeper within the ODZ, to 365 m depth (Fig. 6D). In that year, sinking particle N₂ production rates were variable at the top of the ODZ: 7.32 and 21.09 nM N day⁻¹ at 87 and 85 m depth, respectively. Further within the ODZ, sinking particle rates then decreased at 151 m (4.07 nM N day⁻¹) before increasing to 18.46 nM N day⁻¹ at 220 m and then at 12.09 nM N day⁻¹ at 365 m. As noted above, the overall water column N₂ production rates at St P2 in 2018, which represent production from both sinking and suspended POM in addition to dissolved sources, were generally lower than the sinking particle-only rates, potentially indicating uniquely intense hotspots of N₂ production captured in the incubators (Fig. 6D).

There are two inputs to the overall N₂ production rate from sinking particles, and thus two potential sources for variability: (i) the organic carbon concentration in the experimental +particles chamber and (ii) the measured accumulation of ¹⁵N-labeled N₂ in the chamber. At St P1 in January 2017, *in situ* incubations were deployed in duplicate at four depths at different times: the bottom of the upper oxycline (100 m), just below the SCM (120 m), at the secondary nitrate maximum (150 m), and fully

below the SCM (180 m) (Fig. 6A). For replicate deployments at the same depth, sinking particle fluxes were variable, speaking to the heterogeneous nature of particles over short (days long) collection periods. For a set of repeated depth incubations at 100 m, both organic carbon in sinking particles and N_2 production rate. The two cone sediment trap deployments collected sinking particles at the offshore St P2 for 12 hours before ~ 24-hour incubations, two days apart in January 2017. The trap deployed on January 9th trap collected $37.58 \mu\text{mol C m}^{-2} \text{ day}^{-1}$ and the trap deployed on January 11th collected $115.68 \mu\text{mol C m}^{-2} \text{ day}^{-1}$ (Table S2). There was more labeled N_2 accumulation in the chamber with higher organic carbon flux (15 vs 29 nM N/day), and when these raw rates (Fig S5) were adjusted to represent the N_2 production rate due to sinking particles, they came to 6.99 and 8.80 nM N day^{-1} , respectively, for the January 9th and January 11th incubations (Table S2). Thus, rate variability appeared to be related to variability in sinking organic C fluxes.

Discussion

Most sediment trap deployments last between several weeks to a year (Mouw et al., 2016), resulting in a muting of stochastic signals and short-term variability. Since our sediment trap deployments lasted between one and three days, we can evaluate short-term flux variability and, with use of our combined sediment trap-*in situ* incubators and insight from satellite-derived surface chlorophyll, the consequential metabolic output of this flux variation. We observed that sinking fluxes correlated with satellite-derived productivity rates except when the mixed layer was particularly shallow; the relatively shallow mixed layers with deep light penetration in this system allow most of the biomass to be below the mixed layer. What emerges from our high-resolution observations of sinking particle fluxes and *in situ* N_2 production over three seasons in the ETNP ODZ is a new perspective of carbon and nitrogen dynamics in this ODZ, where fresh organic matter additions at depth create a significant departure from the standard Martin curve and contribute meaningfully to N_2 production within the ODZ.

In many of our flux profiles, a flux inversion was observed, where the flux of sinking particles increased between 100–400 m. If we define a flux inversion as an increase with depth of $> 20 \mu\text{mol C m}^{-2} \text{ day}^{-1}$, then all six flux profiles we collected exhibit such a feature (Fig. 3). In October 2019 at offshore Sts P2 and P3, the observed inverted fluxes were smaller ($28\text{--}66 \mu\text{mol C m}^{-2} \text{ day}^{-1}$ at St P2 and $63 \mu\text{mol C m}^{-2} \text{ day}^{-1}$ at St P3) than the other profiles (Fig. 3). Such flux profile features in other ocean regimes have been associated eddy-driven subduction following transitory events like phytoplankton blooms in the northeastern Atlantic (Omand et al., 2015) or in the high-nutrient, low-chlorophyll Southern Ocean waters following experimentally iron addition-induced blooms (SoFEX site, see Buesseler et al., 2007). In the generally oligotrophic ETNP, while there was no evidence in the satellite-derived NPP of significant surface phytoplankton blooms (Fig. 2), but there was consistently a SCM at the top of the ODZ at St P1 and St P2 which may produce the flux inversion features that we observed.

Thus, there is increasing evidence that the injection at depth of organic matter in the ETNP are at least in part from *in situ* production in the ODZ itself by cyanobacteria. At the offshore St P2 in April 2012, there

was a flux inversion in a three point sediment trap deployment profile, where flux at 150 m was $27 \mu\text{mol C m}^{-2} \text{ day}^{-1}$ greater than that at 105 m (Fuchsman, Palevsky, et al., 2019). In that study, metagenomic analyses showed that the SCM was composed almost entirely of cyanobacteria, as has also been demonstrated using flow cytometry with samples collected in 2014 (Garcia-Robledo et al., 2017). Similarly, metaproteomic analyses of the sinking particles caught in the sediment traps at St P2 in April 2012 showed that cyanobacterial protein was a constituent of sinking particles (Fuchsman, Palevsky, et al., 2019). Cyanobacterial peptides are identifiable in sinking particles at the bottom of the ODZ to a depth of 1000 m at St P2 (Duffy et al., 2022). Depleted $\delta^{15}\text{N}$ in size fractionated organic matter indicated that the ODZ cyanobacteria, which use nitrite depleted in $\delta^{15}\text{N}$, were abundant in $> 500 \mu\text{m}$ particles for 50–100 m below the SCM (Fuchsman & Cram, 2025). The mechanisms by which the small cyanobacterial cells become a part of sinking particles may have to do with viral infection and lysis (Fuchsman, Palevsky, et al., 2019). There is also emerging evidence that zooplankton and/or forage fish may be an important organic matter source in the ETNP ODZ. Recent work, from the same cruises and stations as this study, show signatures consistent with organic matter of zooplankton/forage fish origin in the C:N and $\delta^{13}\text{C}$ of suspended and sinking organic matter at the vertical migration depth (250–450 m) that suggest transportation to these depths by migrating zooplankton/forage fish. The zooplankton migration maximum was coincident with a maximum in the biological N_2 gas and a tertiary nitrite maximum, suggesting the link between migrating zooplankton and N_2 production (Fuchsman et al., 2025). Another possible explanation for an inverted flux profile is lateral transport of sediment from the shelf slope break; the effect of shelf sediments on this station has been proposed from dissolved iron and iodine data (Bolster et al., 2022; Moriyasu et al., 2020). However, beam transmissometer data, which can be used to track sediment into the water column (Gardner et al., 2018), does not indicate a sediment plume at St P1 during our expeditions (Fig S6). Station P2, approximately 300 km from the slope, also had no evidence of a sediment plume.

With or without an observed flux inversion or the depth resolution to capture it, particle flux profiles that deviate from the classic Martin curve have been observed in the ETNP for decades. The classic sinking POC flux profiles from the two ETNP stations of the VERTEX (Vertical Transport and Exchange) study do not, however, show flux inversions. These profiles were obtained using free-floating particle interceptor traps deployed for ~ 22 days in October/November 1981-2 and had attenuation coefficients of 0.805 and 0.648 (Stations II and III, respectively), comparable to the combined open northeast Pacific value of 0.858 (Martin et al., 1987). Later, Van Mooy et al. (2002) observed a flux inversion at a coastal ETNP station in winter/early spring (Feb/March 1999) with a Martin attenuation coefficient (b) of 0.40, indicating a much slower particle attenuation rate than the oxygenated ocean. Using marine snowcatchers rather than sediment traps, Cavan et al. (2017) also observed POC flux increases at intermediate depths for slow-sinking particles in Dec 2013-Feb 2014 at six onshore-to-offshore stations further south in the ETNP (13.0-13.4° N, $\sim 91.2^\circ$ W).

In this work we demonstrate the importance of sinking particles' contribution to overall N_2 production in the ODZ. The incubations performed here were not designed to differentiate between these N_2

production metabolisms, because we only used ^{15}N -labeled nitrite and did not use ^{15}N -labeled ammonium. Rates from sediment trap *in situ* incubators from a previous cruise indicated that when ^{15}N - NH_4^+ was used, there was no increase in N_2 production rates in incubations with sinking particles, but the use of ^{15}N -labeled nitrite, there was an increase (see Supplemental Information and Fig S7 and S8). Given the difficulty of deploying the *in situ* incubators used here, only one chemical species could be ^{15}N labeled; in the ODZ, nitrite is the most logical choice. In the ODZ water column, there have been consistent reports of extra $^{29}\text{N}_2$ produced from ^{15}N -labeled nitrite compared to $^{29}\text{N}_2$ from ^{15}N -labeled ammonium, indicating either an unknown pathway, or denitrification with internal pools of NO_x^- (Chang et al., 2014; De Brabandere et al., 2014; Nicholls et al., 2007). Particles are known to have high internal concentrations of nutrients (Simon et al., 2002). Thus, particles are not a system where we expect ^{15}N -labeled nitrite to be able to properly differentiate anammox and denitrification. Therefore, we choose here to report total N_2 production rates.

While these N_2 production rates are the first measured in any ODZ using *in situ* incubations, there are numerous comparisons in the literature to similar ^{15}N -tracer shipboard incubations, seawater gas and isotope derived rates, and models. Babbin et al. (2014) measured *in vitro* rates in shipboard incubations at the same slope (St P1) and offshore (St P2) in April 2012. When sterilized sinking particles from an earlier version drifting net traps were added to $^{15}\text{NO}_2^-$ tracer incubations of water from the bottom of the upper oxycline (100 m) and the nitrite maximum (150 m) at St P2, the authors measured total N_2 production rates of 9.4 and 21.1 nM N day^{-1} , respectively. At St P1 at the same time of year, their rate measurements in 2012 were much higher than ours in 2018, 45.2 nM N day^{-1} at the bottom of the upper oxycline (60 m) and 42.8 nM N day^{-1} at the nitrite maximum (100 m). This could be in part due to the high variability in NPP at St P1 (Fig. 2).

Shipboard N_2 production rates of denitrification and anammox were measured at similar stations to our St P1 and St P2 in the spring of 2018 at 10 depths ranging from 30 m (above the oxycline) to 1000 m (Tracey et al., 2023). Using water sampled directly from CTD Niskin bottles, they found that the magnitude of anammox and denitrification was almost always less than 20 nM N day^{-1} , much lower than rates of nitrate reduction and nitrite oxidation, which they also measured. At their coastal St PS3 (17.68 °N, 102.35 °W), somewhat closer to shore than our slope St P1 (20.15 °N, 106.00 °W), rates of denitrification were mainly undetectable within the ODZ except at 500 m, where they were 5 nM N day^{-1} . Anammox rates were between double that of denitrification at 500 m (10 nM N day^{-1}) and 5.2 and 0.72 nM N day^{-1} at 100 and 150, respectively. While our *in situ* incubations went only as deep as 190 m at our slope St P1, our total N_2 production rates also in April 2018 were higher than those measured by Tracey et al. at similar depths in the upper ODZ: they measured 5.2 nM N day^{-1} at 100 m while our water column and sinking particle rates at 93 m were 14.0 and 13.0 nM N day^{-1} , respectively. They measured a total rate of 0.72 nM N day^{-1} at 150 m while our 150 m water column and sinking particle rates were 53 and 7.4 nM N day^{-1} , respectively, and their combined rates at 260 m and ours at 193 m were near each

other (15 and 8.0/7.0 nM N day⁻¹, respectively). Overall, while the shipboard/CTD-sampled water incubations and our dataset are in the same ballpark, our water column rates were consistently higher. Our previous data from 2013, where *in situ* incubators and shipboard measurements were made simultaneously, also found higher rates with the *in situ* incubator (Fig S9). This is likely because our sampling method included all the particles in the water column, while when using a CTD for sampling, large particles sink below the Niskin bottle sampling port (Suter et al., 2017).

To compare our instantaneous N₂ production rates to rates derived from the N_{def} or N₂:Ar approaches, we multiplied our rates (nM N day⁻¹) by the average age (or replacement time) of water in the ETNP suboxic zone to yield the integrated N loss in μM N, comparable to N_{def}. For all depths, we used the average water age from (DeVries et al., 2012), which was derived by constraining their global ocean circulation model with CFC-11 concentrations and was determined to be 3.9 ± 0.8 years. Integrating N₂ production rates from this study by volume and residence time for the ODZ waters allows us to better compare to earlier rate determinations derived from the DIN deficit (N_{def}) and N₂:Ar ratio approaches (Chang et al., 2010, 2012; Fuchsman et al., 2018). The N_{def} approach estimates rates based on the deficit and an assumed residence time and assumes a constant N:P ratio of the remineralized organic matter. Similar to the *in situ* incubations presented here with ¹⁵NO₂⁻ tracer, the N_{def} method cannot account for reduction of N species, other than nitrate and nitrite (i.e. organic nitrogen) which could also contribute to cycling in low oxygen systems (Devol et al., 2006). To compare our instantaneous rates to total N loss estimates for the ETNP, we scaled our rates by volume estimates for the ODZ. Using a recent estimate of 3.86 ± 0.01 10⁶ km³ from Kwiecinski & Babbin (2021) that we adjusted for the top 400 m of the water column, our average sinking particle and water column rates estimate a total annual N loss of 24.0 Tg N y⁻¹ for sinking particles and 40.7 Tg N y⁻¹ for water column and sinking particles combined, respectively, in general agreement with estimates based on N_{def} of roughly 25 Tg N y⁻¹ (Codispoti & Richards, 1976; DeVries et al., 2013). While our cumulative annual rates could be underestimates due to the exclusion of the deeper ODZ, a shipboard + ¹⁵NO₂⁻ incubation of water from 500 m at a station equivalent to our St P2 suggested low N₂ production rates (< 2 nmol N L⁻¹ day⁻¹) in the deep ODZ below 400 m (Babbin et al., 2014), and biological N₂ gas profiles indicate production from 100–350 m, but a decrease in the deep ODZ (Fuchsman et al 2018; Chang et al 2012).

Our observations point to sinking particle hotspots of N₂ production within the ODZ. In order to probe how sinking particle organic matter attenuation or injection related to N₂ production rates, we calculated the difference (delta) of POC flux from sediment trap profiles as well as the estimated maximum C required for the measured to be N produced in both in the total water column and due to sinking particles (Fig. 7). We employed a ratio of 1.122 mol C consumed per mol N-N₂ produced (Anderson, 1995) to estimate this maximum C requirement, assuming heterotrophic denitrification is responsible for 70% of overall N₂ production (Devol, 2003; Babbin et al., 2014). Looking at the data in this manner, flux increases with depth are rendered as negative flux deltas and indicating where sinking particles were added to the water column both beneath the SCM and the zooplankton vertical migration depths. If

attenuating sinking particles were the primary source of C fueling N_2 production, we would expect to see agreement between the flux delta and sinking particle C requirements, and this is generally the case for incubations above the SCM (Fig. 7). However, most notably in 2018 at both St P1 and P2, the highest measured N_2 production rates corresponded to negative flux deltas, where sinking particles were added to the water column beneath the zooplankton vertical migration depth (~ 200 m) at St P1 and beneath the SCM (~ 150 m) at St P2 (Fig. 7). These data indicate that, in this system, *in situ* sources of organic matter produce the highest N_2 production rates. While there are large assumptions in this comparison, these findings indicate the potential importance of determining the ubiquity, persistence, and future of features like the SCM and zooplankton vertical migration depth.

Our new approach using *in situ* experimentation using incubating sediment traps solidifies the link between particulate OM and N_2 production in the ETNP. Here we demonstrate that sediment trap-incubator systems can be used to enable both particle flux measurements and controlled, *in situ* measurements of N_2 production within an ODZ, with results that are slightly larger than shipboard measurements but generally agree with the DIN-deficit approach. We also highlight *in situ* sources of organic matter as fueling high N_2 production rates, which has several implications for a changing ocean. As the top of the ODZ shoals (Horak et al 2016; Evans et al 2023), the area of the ODZ with light penetration is projected to expand, increasing the instances of a SCM in the ODZ and therefore increasing potential N_2 production rates. These *in situ* sources of organic matter allow N_2 production to occur in oligotrophic anoxic regions, meaning that expansions of ODZs into oligotrophic waters will still increase N_2 production. Additionally, Deutsch et al. (2004) proposed a negative feedback loop where increased N_2 production causes N limitation in surface waters, therefore reducing sinking organic matter which would in turn reduce N_2 production and maintain a balanced oceanic N budget. However, the importance of *in situ* organic matter sources to N_2 production partially negates this negative feedback loop. Thus, as a whole, *in situ* sources of organic matter increase future potential ODZ N_2 production rates compared to a system governed by surface-derived sinking particles alone. This could have implications for future global N budgets.

Methods

Sites and expedition timing

Samples were collected in the ETNP at three different stations: St P1, a slope ODZ station (~ 50 km from shore at 20.15°N , 106.00°W ; water depth 2200 m); St P2, an offshore station in the heart of the ODZ (16.58°N , 107.05°W , water depth 3600 m); and St P3 at the northern boundary of the ODZ (21.99°N , 109.90°W , 3200 m) (Fig. 2). Weeklong station occupations took place at St P1 and St P2 on board the *R/V Sikuliaq* between January 8–13, 2017 (cruise ID: SKQ201617S) and on board the *R/V Roger Revelle* between April 15–27, 2018 (RR1805). An 8-day occupation of St P2 and a 3-day occupation of St P3 took place on board the *R/V Kilo Moana* between October 3–18, 2019 (KM1920).

On all expeditions, a Seabird 911 Conductivity Temperature Depth (CTD) meter was deployed on a CTD Rosette along with the following sensors: a Seabird SBE 43 Dissolved Oxygen Sensor; a WETLabs ECO Chlorophyll Fluorometer (SeaPoint fluorometer on RR1805); a Biospherical/Licor PAR/Irradiance Sensor; and a WETLabs C- Star Transmissometer. Nutrient samples were filtered through Sterivex polyethersulfone membranes (pore size 0.2 μm) before analysis of filtrate using the US-JGOFS protocols (http://usjgofs.whoi.edu/protocols_rpt_19.html) at the University of Washington Marine Chemistry Laboratory.

Net primary production measurements

MODIS satellite chlorophyll (R2022) and satellite-based estimates of net primary production (CAFE model; Silsbe et al., 2016) for the 8-day windows containing 9 January 2017, 15 April 2018 and 8 October 2019 (available from <http://www.science.oregonstate.edu/ocean.productivity>) were extracted from a $1/3^\circ$ box around each station (Fig. 1A). For additional context, monthly data products were also downloaded for the same $1/3^\circ$ box around each station from December 2016 to December 2019 (Fig. 1E).

Total chlorophyll measurements

Water samples were collected on cruises SKQ201617S, RR1805, KM1920 via Niskin bottles mounted to a CTD rosette, where 1 L from each depth was filtered onto a GF/F filter before flash-freezing at 80°C and later processed using a Turner Designs TD-700 fluorometer (Turner Designs, Sunnyvale, CA, USA) using the direct concentration method. For St P2 in 2017, 10 μm , 2 μm polycarbonate and GF/F filters were sequentially filtered and, for our purposes, the values from these three filters were combined to obtain a calculated total chlorophyll.

Sediment trap-in situ incubator design and function

Free floating, surface-tethered sediment traps were used to quantify carbon and nitrogen fluxes from sinking particles and performed controlled, *in situ* N_2 production experiments on sinking particles. Arrays consisted of a surface float with 1–3 trap-incubation systems set to desired depths which were allowed to drift with surface currents, during which time they collected and incubated sinking particles. Traps deployments lasted for between 21 and 93 hours. Generally, deeper traps were left out for longer periods to collect more material. Two types of traps were deployed in 2017 and 2018 (cone and net) and two types of sediment trap were deployed in 2019 (cone-net hybrid and net, see Fig S8). The unpoisoned trap-incubator design (Fig. 1) collected particles using either a hard plastic cone or mesh net design similar to Peterson et al. (2005) and Van Mooy & Keil (2015). The aspect ratios, or height/trap mouth diameters, of the cone, net, and hybrid traps were 0.6, 2.5, and 1.7, respectively (for additional trap dimensions, refer to Fig S10). Despite these differences, the plastic cone and mesh net trap styles were

demonstrated to have similar collection efficiencies in the ETNP in 2017 (Cram et al., 2022). The relatively low aspect trap design does not cause particles to be released during system collection due to pre-collection cod end closure at depth (Event 4, see below).

The gate valves at the tops and bottoms of the incubation chambers, as well as the plungers of ^{15}N tracer-injecting syringes, were held open with tensioned rubber tubing restrained with nylon-jacketed electronic dissolving links (“burn wires”) prior to deployment. The chamber gate valves and syringes were controlled using a preprogrammed onboard Arduino microcontroller that directed current from two 9V alkaline batteries to individual electronic dissolving links. The nylon jacket on the electronic dissolving link was stripped at 1-cm wide sections which held open a gate valve or syringe plunger. When current was applied by the Arduino microcontroller, the electronic dissolving links corroded in seawater and released either the attached gate valves or syringe plungers. Sediment trap incubators were deployed with all gates open to facilitate the dissipation of any trapped air bubbles during an 8-hour acclimation period in anoxic waters at the target depth.

Particles collected in the trap fell into a vertically-oriented 1 L incubation chamber (“+particles chamber”) that was initially open on both ends. Another vertically-oriented 1 L incubation chamber (“water column chamber”) sat to the side of the sediment trap and was deployed open on both ends but closed immediately before incubation. The bottom of the +particles chamber was programmed to close after the 8-hour acclimation period at the target depth, beginning a collection phase of 12–96 hours. After the collection phase, the top of the +particles closed, along with both top and bottom of the water column chamber. At the beginning of the incubation phase, ^{15}N -labeled nitrite was injected into both +particles and water column chambers. A second 500 mL collection chamber (“top collector”) immediately above the +particles chamber collected additional sinking particles during the incubation phase for use in flux calculations. For deployments shallower than 250 m, trap systems were equipped with sensors for pressure, temperature, pH, and O_2 (Yellow Spring Instruments EXO² sonde and sensors; Xylem, Yellow Springs, OH USA) within the two incubation chambers primarily to monitor for potential oxygen contamination from bubbles, of which there was no evidence (Fig S11).

Sediment trap flux measurements in the ETNP

Particles collected in the net or cone fell into one of two chambers (Fig. 1). The bottom chamber collected particles from the net and incubated them, and these samples were generally not used in flux analyses. The top chamber collected particles during the incubation (20–28 hours) for flux measurements, after which the arrays were recovered. In a few instances, the top chamber C and N fluxes were not available, and bottom (+ particle incubation) chamber fluxes were used. No poisons were used in any chamber, and in the few cases ($n = 2$) where living zooplankton, or ‘swimmers’, entered the collection chamber at the more oxygenated depths, they were manually removed upon trap recovery. Zooplankton carcasses were retained and photographed but removed before the organic matter analysis; these carcasses will be examined in a separate paper. Sediment trap material was filtered

immediately upon trap recovery onto pre-combusted glass fiber GF-75 (0.3 μm) 45 mm filters and preserved until further analysis at -80°C.

Carbon and nitrogen measurements

Carbon content of particles in each trap was measured by elemental analyzer-isotope ratio mass spectrometry (EA-IRMS, Nakatsuka et al., 1997). Elemental analyses for particulate carbon and nitrogen quantities as well as $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotopic compositions were conducted at the University of California Davis Stable Isotope Facility and the University of Washington IsoLab on freeze-dried, homogenized sediment trap samples in duplicate. Filtered sediment traps samples were freeze-dried and subsequently pulverized in 2 mL low-bind plastic tubes using a FastPrep Homogenizer beadbeater, and then fumed with acid to remove carbonates. Samples were packed into silver capsules and stored at room temperature before analysis by an elemental analyzer attached to an IRMS, either a Elementar Vario EL Cube attached to a Isoprim VisION mass spectrometer (University of California, Davis) or Costech attached to a ThermoFinnegan MAT 253 mass spectrometer (University of Washington). Sediment trap C and N fluxes from St P2 in 2017 have already been published (Cram et al., 2022; Fuchsman et al., 2025).

Suspended organic C and N concentrations for 2018 and 2019 are previously reported (Fuchsman et al., 2025; Fuchsman & Cram, 2025). Samples for suspended organic C and N concentrations for 2017 were obtained from 4 L of seawater filtered onto pre-combusted GF/F filters. Samples were wafted with HCl for 24 hours and then packaged in both silver and tin capsules. For St P2, samples were analyzed at the University of Washington and for St P1 samples were analyzed at University of California, Davis, both as indicated above. Additionally, twelve samples across both stations were run at the Central Appalachian Stable Isotope Facility at the University of Maryland Center for Environmental Science using a ThermoFisher Delta V + and a Carlo Erba NC 2500 Elemental Analyzer.

Profiles of sinking particle fluxes were fit to a normalized power function below as first described by Martin et al. (1987) (Eq. 1):

$$F_z = F_{z_0} \left(\frac{z}{z_0} \right)^{-b} \quad (\text{Eq. 1})$$

In this equation, F_z is the flux at a given depth z , normalized to a reference depth z_0 . We used the bottom of the upper oxycline as the reference depth. This was where O_2 reached below $10 \mu\text{mol kg}^{-1}$ and ranged from 73–100 m (more consistently where $\sigma_\theta \sim 25.7$). We believe this is the most biogeochemically relevant parameter in the system, with both microbial and zooplankton oxygen limitations a key hypothesized explanation for diminished flux attenuation (Devol & Hartnett, 2001; Keil et al., 2016; Van Mooy et al., 2002) in this ODZ.

In situ N₂ production incubations

Onboard the sediment trap-*in situ* incubator systems, a final concentration of 40 $\mu\text{mol L}^{-1}$ ¹⁵N-nitrite tracer was added to the +particles and water column experimental chambers. This tracer was de-oxygenated before use; however, it was likely to acquire small amounts of oxygen in the syringe during deployment. Therefore, dithiothreitol (2 $\mu\text{mol L}^{-1}$ final concentration) was added to the syringe to scrub potential minor O₂ contamination from the tracer. We were extremely careful that there were no bubbles in the syringe or tubing leading from the syringe to the incubation chamber. High tracer concentrations increased the likelihood of the tracer diffusing into the particles, as evidenced by Babbin et al. (2020), which showed that adding nitrite to ODZ waters that already had nitrite present did not increase N₂ production rates (Babbin et al., 2020).

Immediately after returning the sediment trap-*in situ* incubator systems shipboard, the experimental chambers were sampled using single-use needles into 12 mL septum-capped glass Exetainer vials (LabCo, UK) that had been purged with helium gas for 5 minutes. Duplicate vials were sampled for each incubation. Vials were poisoned with 50% (w/v) zinc chloride and stored in the dark at room temperature. Water from CTD casts was collected into Exetainers to measure the background isotopic composition of N₂ gas by overfilling the exetainer four times and closing the exetainer with a needle inserted to just below the septa, to cause any bubbles to be removed during closing. Each Exetainer was checked for bubbles. Exetainers were measured for ²⁹N₂ and ³⁰N₂ accumulation on a Thermo Delta V IRMS in continuous flow mode using helium gas. Each datapoint was background-corrected. A tank of N₂ gas was the internal standard and was measured three times during each sample measurement. Each sample was measured three times. Air was used as an external standard and was added to helium purged Exetainers using a range of volumes. These air standards were measured regularly throughout the run to quantify any drift. Rate measurements were calculated following de Brabandere et al. (2014) using incubation durations and the volumes of the experimental chambers.

Suspended organic matter from the water column chamber was measured but was below detection limit since the water column chamber only contained 1 L of water. Suspended organic matter concentrations from these stations, where 4 L of water were filtered, are available and were generally in the range of ~ 0.1–3.3 $\mu\text{M C}$ (Fig. 4; Fuchsman et al., 2025; Fuchsman & Cram, 2025).

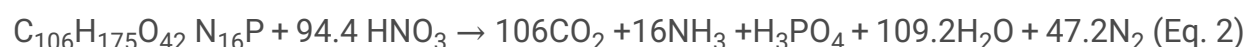
N₂ production normalization

The goal in the incubations was to arrive at N₂ production rate values that represented 1) the overall N₂ production rate in the water column, which was obtained from the water column chambers; and 2) the N₂ production rate due solely attributed to the sinking particles in the water column (Fig. 1). Because the incubations occurred with particles that had been collected over a 12-hour period, we thus adjusted the initial rates in the +particles chambers (conceptually visualized Fig S12) to account for this

concentration factor and arrive at an adjusted rate relevant to the actual concentration of particles in the water column. To do this, we adjusted the labeled N_2 accumulation rate in the +particles chamber to be the rate for the mass concentration (m/V, in $\mu \text{ mol organic C/m}^3$) for sinking particles in the water column at the target depth. This concentration ($\mu \text{ mol C m}^{-3}$) was determined using the calculated fluxes of organic carbon in sinking particles ($\mu \text{ mol C m}^{-2} \text{ day}^{-1}$) derived from the sediment traps (Fig. 3) and the average sinking rate of particles (m day^{-1}). While particle sinking rates were not directly measured during our cruises; we used a value for sinking particles in the ETNP ODZ determined with a particle settling column from Cavan et al. (2017) who reported the ratio of slow sinking vs. fast sinking particle flux to be 18:0.6, with sinking rates measured at a range from 6.5 m day^{-1} and 69 m day^{-1} . We therefore used an average sinking rate value of 8.45 m day^{-1} in these adjustments. The mass concentration of organic carbon in sinking particles at depth ($\mu \text{ mol C m}^{-3}$) was then used with the actual concentration organic carbon in the top collector chamber ($\mu \text{ mol C m}^{-3}$) to calculate a unitless 'concentration factor' that was used to adjust the initial N_2 production rates (nmol N day^{-1}) to account for this factor and arrive at the N_2 production rate due to sinking particles (nmol N day^{-1}). We did not account for suspected particles in the chamber, which were generally in the range of $\sim 0.1\text{--}3.3 \mu \text{ M C}$ at Stations P1 and P2 in the ODZ in 2018 and 2019 (Fuchsman et al., 2025; Fuchsman & Cram, 2025) and well under 10% of organic carbon concentrations calculated. See Raven et al. (2021) for a similar particle normalization approach and an example calculation in Fig S12.

We performed two additional calculations with this data. First, we used the residence time of the water in the ODZ (DeVries et al 2012) to match N_2 production rates with N deficit estimates of biologically produced N_2 gas. Most N deficit calculations shown here have been published (Fuchsman et al., 2025), but values for St P3 are new to this publication. The N deficit is a variation on N^* that uses N:P ratios from nearby oxic waters, where the ratio is 14, rather than assuming a ratio of 16 (Chang et al., 2012). The N deficit matches measured biological N_2 gas concentrations closely in the ETNP (Chang et al., 2012; Fuchsman et al., 2018).

Secondly, we used a nitrogen balance to estimate the required organic carbon required to satisfy our observed N_2 production rates assuming an elemental stoichiometry based on Anderson (1995) and the balanced equation for denitrification from Paulmier et al. (2009), similar to the approach of Fuchsman et al., (2015) (Eq. 2) So that molar quantity of C required for observed N_2 production is $\frac{106}{(47.2 \times 2)} \text{ N.} :$



Declarations

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Conflict of Interest

The authors declare no conflicts of interest.

Author contributions

MED and CAF wrote the original manuscript with input from all co-authors. RGK, WR, and AHD designed the *in situ* sediment traps incubators. CAF, MED, and GR collected and analyzed samples. AHD, and RGK supervised incubator trap deployment. HIP and MED analyzed satellite data.

Data availability

CTD and nutrient data can be found at BCO-DMO for the R/V *Sikuliaq* (dataset 732092), the R/V *Revelle* (dataset 779185), and the R/V *Kilo Moana* (dataset 849710) cruises. BCO-DMO repositories are available for sediment trap fluxes (DOI:10.26008/1912/bco-dmo.948735.2), suspended organic matter (DOI:10.26008/1912/bco-dmo.948637.2), and N₂ production rates (DOI: 10.26008/1912/bco-dmo.1002907.1). MODIS satellite chlorophyll and satellite-based estimates of net primary production are available from <http://www.science.oregonstate.edu/ocean.productivity>.

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Figures

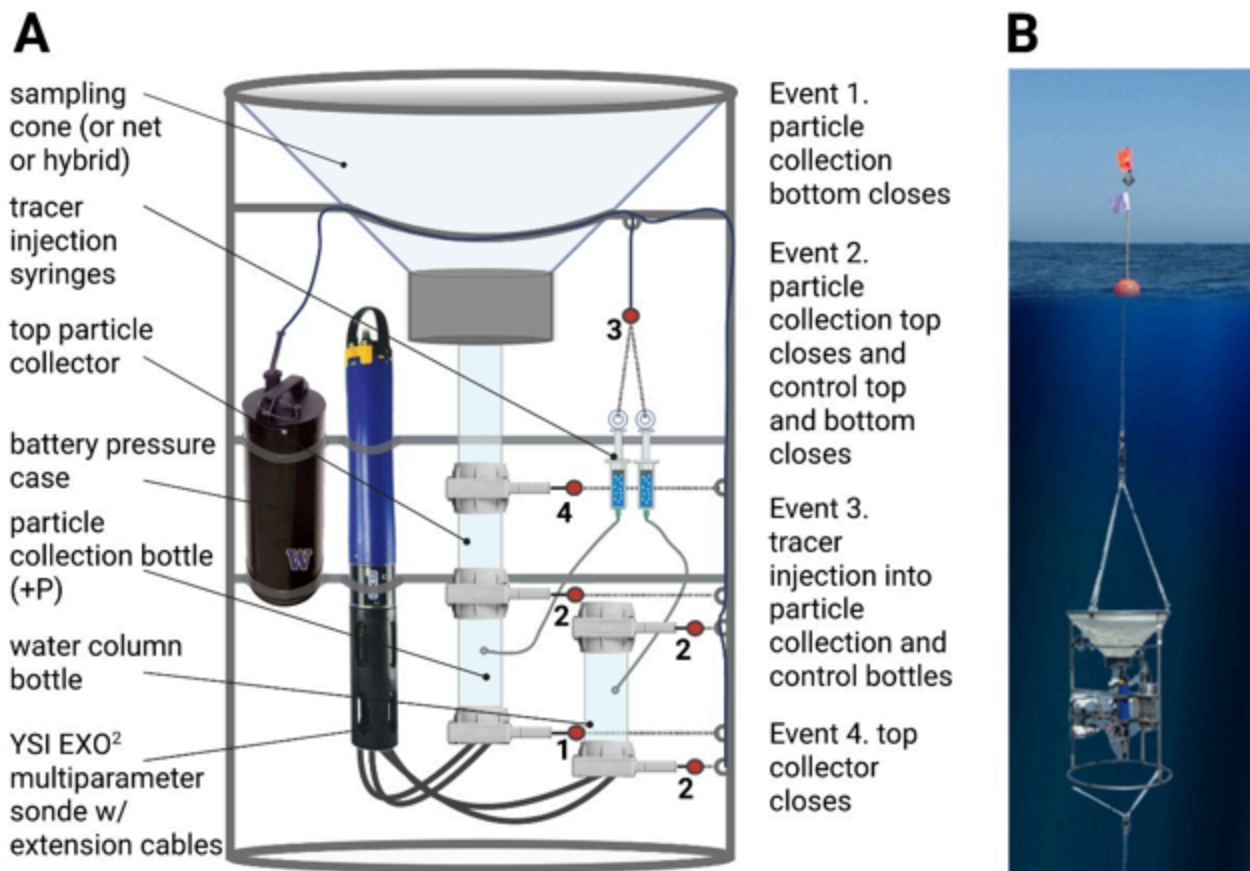


Figure 1

Design of sediment trap-in situ incubation systems. Example of a trap-incubator with component descriptors (A): This diagram shows the plastic cone trap system. Components across all trap-incubators are the particle collection chamber (+particles), water column chamber, and top particle collector chamber. The +particles and water column chambers are monitored by in-chamber pH and dissolved oxygen sensors connected by extension cables to a YSI EXO² sonde. A pressure case containing a pre-programmed Arduino microcontroller and 9V alkaline batteries controls all gate valves and tracer injection syringes. The +particles and water column chambers are deployed open; after

reaching the target depth, the system equilibrates for 8 hours with all gate valves open to dissipate any air bubbles that would lead to oxygen contamination. After 8 hours, the gate valve at the bottom of the +particles chamber closes (**Event 1, denoted with red circles**), allowing sinking particles to collect for a pre-programmed period of time. Next, the top gate valve of the +particles chamber closes simultaneously with the top and bottom gate valves of the water column chamber (**Event 2**). After 15 minutes, the syringes inject tracers into each chamber (**Event 3**). After the incubation period, during which particles continue to collect in the top particle collector chamber, the gate valve at the top of that chamber is closed (**Event 4**) before system recovery. The two other trap system types are conical net traps and hybrid canvas extension cylinder-cone traps; all incubation components are identical across designs. **B:** Cartoon of free-floating, surface tethered trap-incubator systems with mast, floatation buoy, radar reflector, AIS buoys and satellite trackers. Between one and three trap-incubator systems were deployed in vertical arrays with line lengths used to meet target depths. Diagrams not to scale, see Supplementary Information for additional incubator design details.

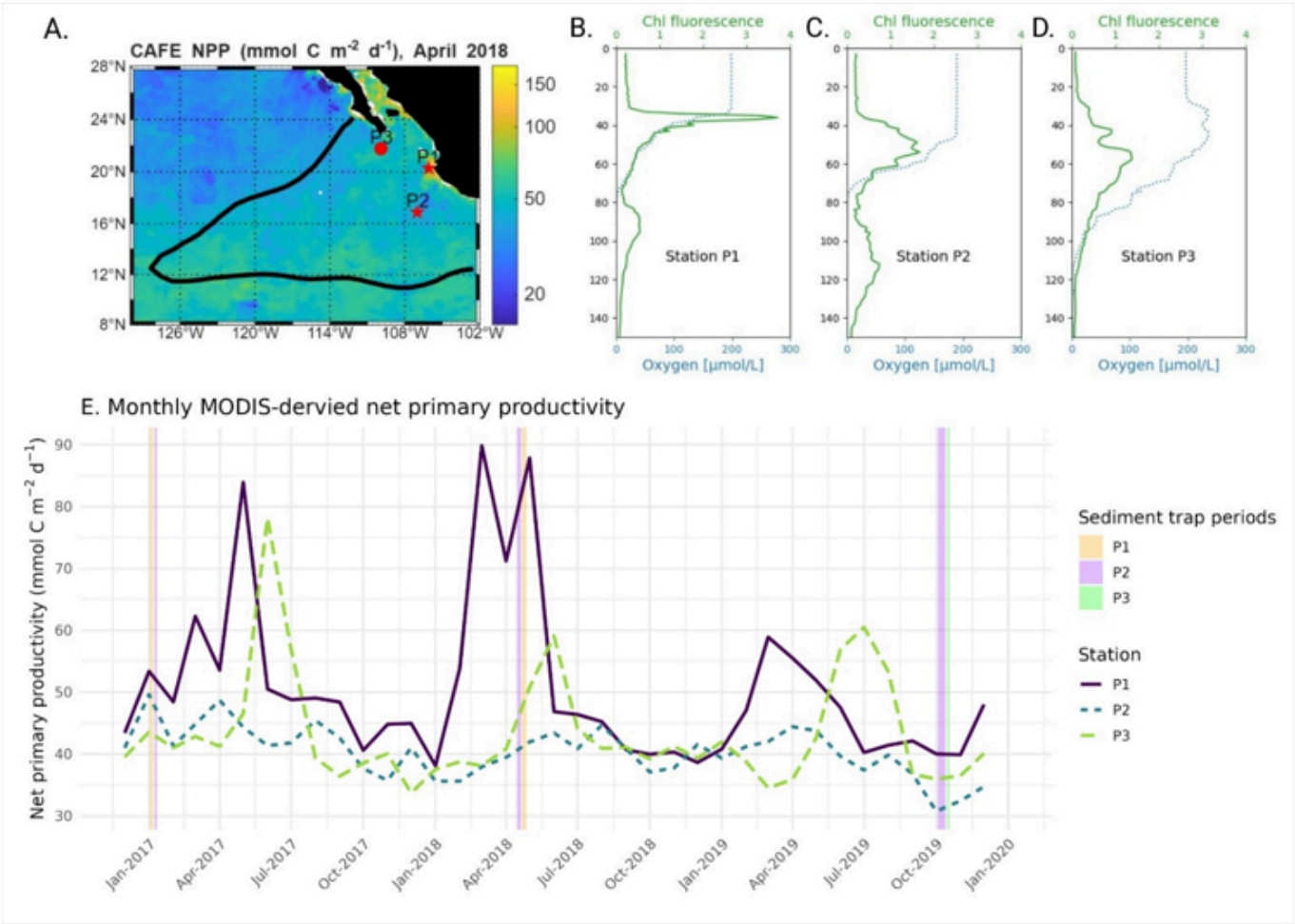


Figure 2
Locations of stations P1, P2, and P3 in the eastern tropical North Pacific oxygen deficient zone (ETNP ODZ) (A) with exemplary station chlorophyll and O₂ profiles (B-D). Monthly surface net primary

production (NPP) derived from MODIS satellite estimates at sediment trap deployments sites from December 2016 to December 2019 with sediment trapping periods in January 2017, April 2018, and October 2019 denoted for each station (E). The black line in (A) indicates the 10 μM O_2 ODZ boundary as determined from the World Ocean Atlas.

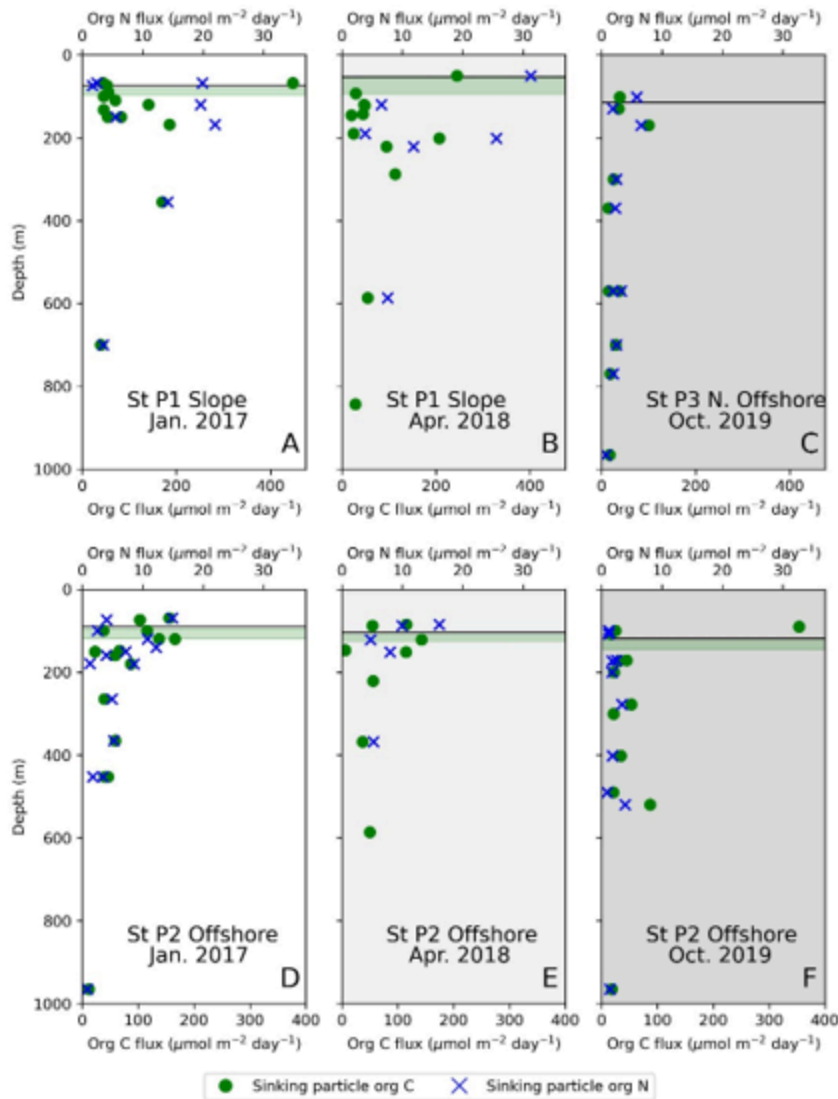


Figure 3

Organic carbon and nitrogen fluxes in sinking particles at onshore and offshore stations. Fluxes of organic carbon and organic nitrogen in sinking particles at the onshore ODZ station P1 in January 2017 (A) and April 2018 (B); the northern edge ODZ station P3 in October 2019 (C); and the offshore central ODZ station P2 in January 2017 (D) and April 2018 (E) and October 2019 (F). Horizontal black lines denote the onset of anoxia and green shadings represent the approximate depth and thickness of the secondary chlorophyll maxima (there is no detectable secondary chlorophyll maximum at St P3).

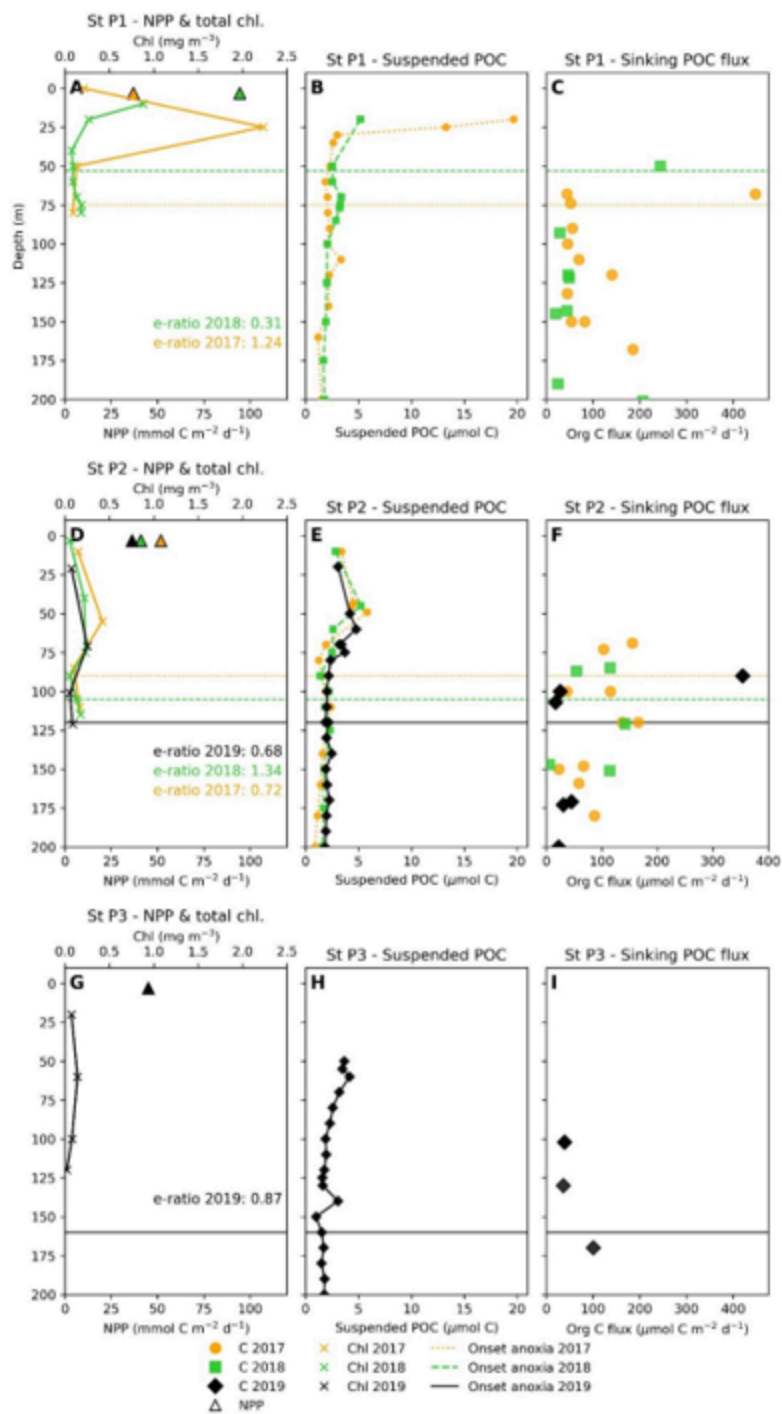


Figure 4

Surface net primary productivity (NPP) derived from 8-day average MODIS satellite-based estimates (triangles) and total chlorophyll (x markers), suspended particulate organic carbon (POC) profiles, and sinking POC flux profiles from sediment trap deployments.

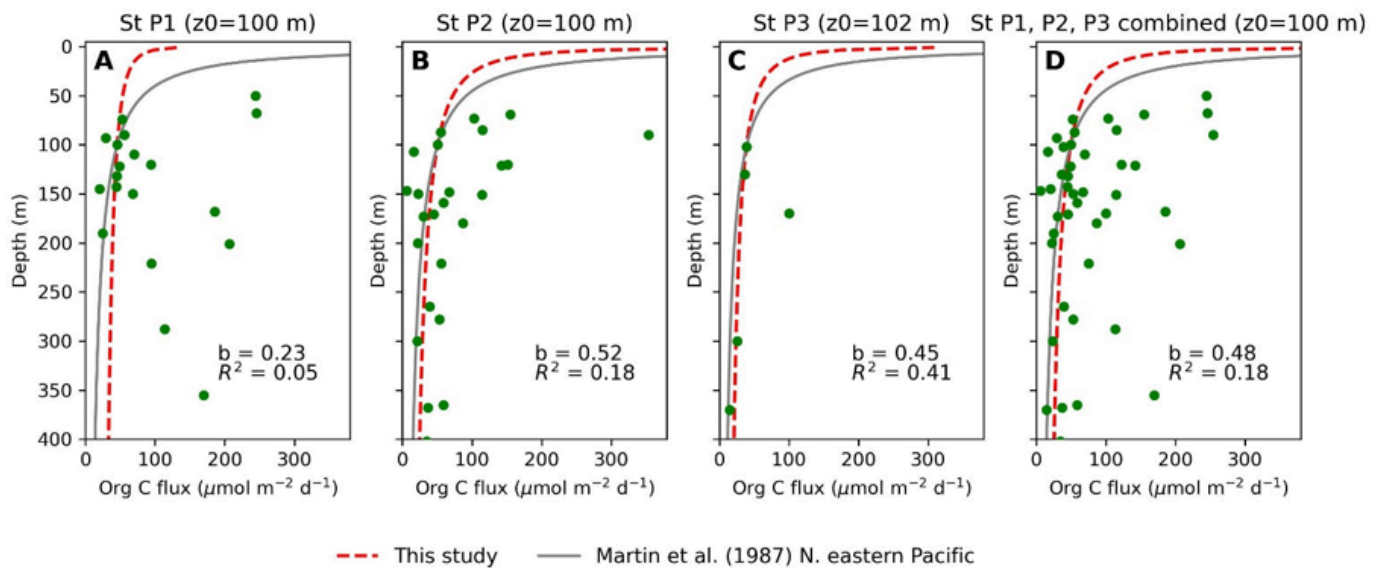


Figure 5 Multi-year sediment trap organic carbon fluxes at ETNP ODZ Stations (A) P1 in January 2017 and April 2018; (B) P2 in January 2017, April 2018, and October 2019; (C) P3 in October 2019; and (D) in all stations for all years ($n = 70$). Fluxes were fit to a Martin-type normalized power function $F_z = F_{z_0} \left(\frac{z}{z_0}\right)^{-b}$ (red dashed lines) where the reference depth, z_0 , was as close to 100 m as possible given the sample set with poor R^2 values. Martin et al. (1987) open ocean composite organic fluxes data derived from the means of replicates at depths between 100 and 2000 m at Stations 2, 4, 5, II, III, and NPEC in the northeast Pacific ($R^2 = 0.81$, $n = 48$).

Figure 5

See image above for figure legend.

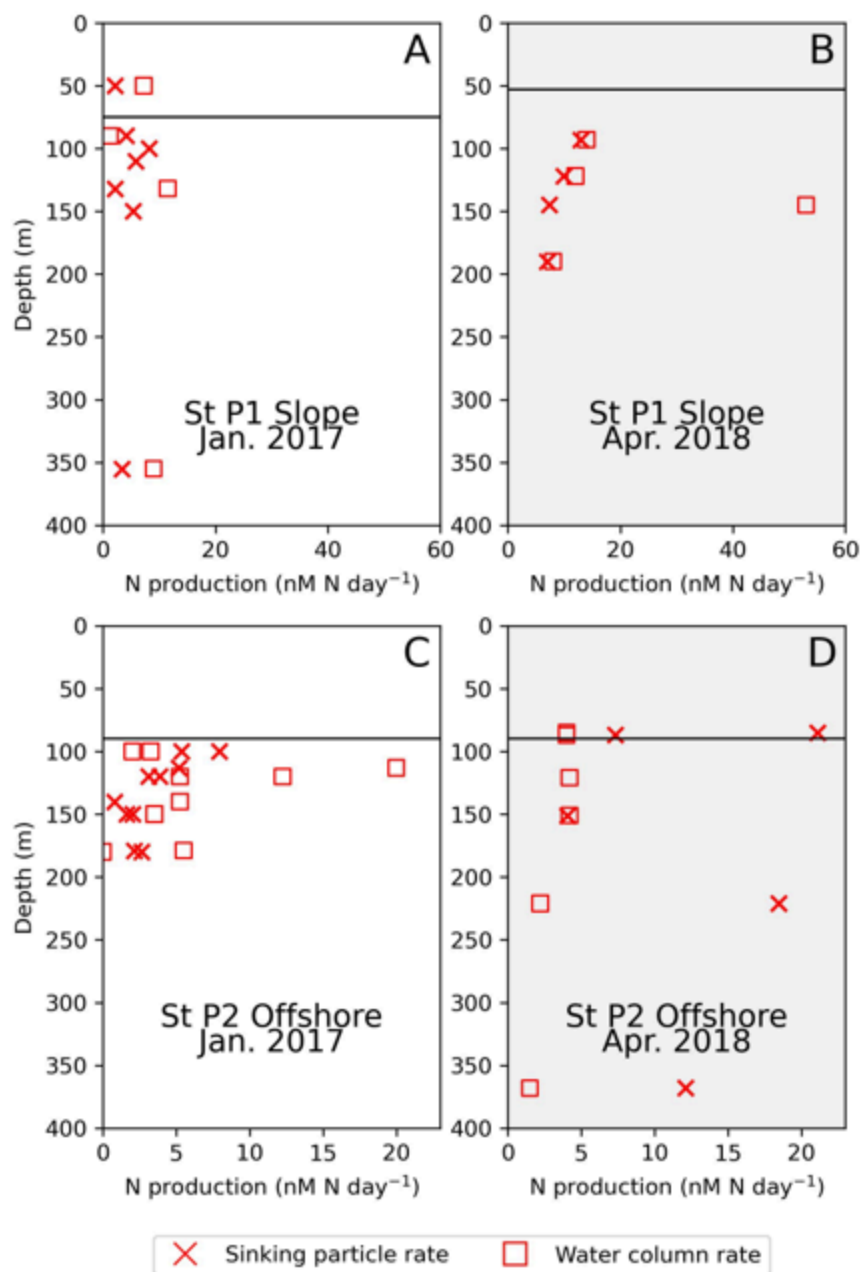


Figure 6

Rates of N_2 production as measured from in situ incubations with concentrated sinking particles in the ETNP ODZ. N_2 production rates adjusted to account just for rates due to sinking particles (red x markers) and the water column, which represents production from both sinking and suspended POM in addition to dissolved sources (empty red boxes), from deployments in January 2017 (A, C) and April 2018 (B, D) at an onshore and offshore station. Horizontal black lines denote the onset of anoxia.

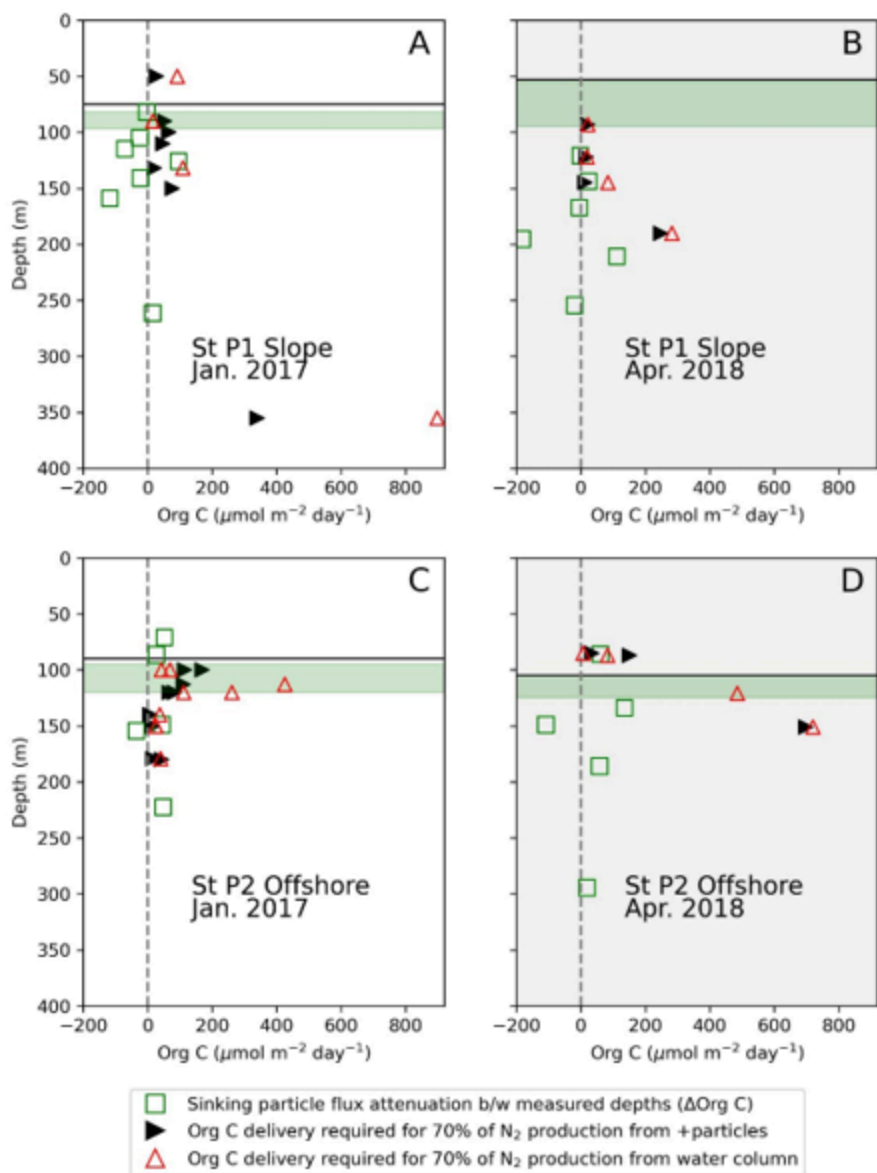


Figure 7

Organic carbon flux attenuations compared to the organic carbon required if 70% of observed N_2 production in incubations was from heterotrophic denitrification. We calculated the organic carbon sinking particle flux attenuations (green squares) as the difference between successive sediment trap fluxes with depth for onshore St P1 in January 2017 (A) and April 2018 (B); and for offshore St P2 in January 2017 (C) and April 2018 (D). We then compared these flux attenuations to the organic carbon that would be required to fuel 70% of observed N_2 production from our in situ incubations, integrated for the same depth ranges as the flux attenuation calculations (black triangles for the +particles incubations and red triangles for the water column incubations). Negative flux attenuations (>0) represent when flux increases with depth, often beneath the secondary chlorophyll maximum shown as green shaded bands. Horizontal black lines denote the onset of anoxia. Note that there were no successful N_2 production incubations in 2019.

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- [TableS120260907.xlsx](#)
- [TableS320260907.xlsx](#)
- [DuffySupplementalInformation20260907.docx](#)