



Stoichiometry of marine gels cycling in the North Pacific Subtropical Gyre: Insights on
subsurface preformed nitrate anomalies

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Abstract

Transparent exopolymer particles (TEP) and Coomassie-stainable particles (CSP) are gel-like exopolymers produced by phytoplankton and bacteria through the release of dissolved organic matter (DOM) into the water column. Despite their abundance (up to 10% of dissolved organic carbon in the ocean is in the form of gels) their behavior and role in the ocean's carbon cycle is not fully understood. TEP and CSP cycling may influence upper ocean carbon (C), oxygen (O₂), and nitrogen (N) budgets, but data on their biogeochemistry is lacking. Within the North Pacific Subtropical Gyre (NPSG), cycling of TEP and CSP has been hypothesized to help explain linkages between subsurface nitrate and oxygen fields and mixed-layer summertime dissolved inorganic carbon (DIC) drawdown. This study provides empirical estimates of TEP and CSP formation rates, remineralization rates, and C:N:O₂ stoichiometry during a June 2021 cruise from Station ALOHA (22°45') to 31°N in the NPSG. Incubation experiments at 5 m and 125 m revealed TEP accumulation at Station ALOHA and TEP net remineralization at 31°N. CSP showed net remineralization across most depths and stations. Divergent cycling patterns between TEP and CSP suggest distinct roles within the exopolymer pool. The calculated exopolymer remineralization stoichiometry—C: N of 19.4:1, O₂:C of 2.7:1, and O₂:N of 52:1—indicates elevated oxygen demand relative to carbon and nitrogen, helping to explain ~15-20% of the region's subsurface preformed nitrate anomalies. By constraining the elemental stoichiometry of TEP and CSP and their patterns of change across depths and locations, this study highlights the importance of exopolymer cycling within upper ocean carbon, oxygen, and nutrient budgets within the NPSG.

1. Introduction

Subtropical oceans are one of the largest biomes on Earth covering ~60% of the ocean surface. These regions are typically characterized by low macronutrient and low euphotic zone chlorophyll a concentrations, which lead to low levels of net primary productivity (Behrenfeld and Falkowski, 1997), earning the moniker of 'ocean deserts'. However, numerous net community production (NCP) and total annual carbon export estimates from the subtropical ocean suggest that the biological carbon pump strength is similar to mesotrophic ocean regions receiving greater vertical nutrient fluxes (e.g., Emerson, 2014; Gruber, 1998; Karl et al., 2021;



Quay et al., 2020; Quay & Stephens, 2025; Roshan & DeVries, 2017; Teng et al., 2014). Decades
55 of observations at the Bermuda Atlantic Time-series (BATS) and Hawaiian Ocean Time (HOT)
series sites have noted a variety of nutrient supply mechanisms to the subsurface, such as N₂
fixation, vertical mixing events, atmospheric deposition, lateral transport. However, these
mechanisms fail to fully explain the observed moderate summertime dissolved inorganic carbon
(DIC) drawdown that these subtropical regions experience (Chow et al., 2017; Fawcett et al.,
60 2018; Johnson et al., 2010; Karl et al., 2021; Letelier et al., 2019; Letscher and Villareal, 2018).
In addition to the anomalous DIC to nutrient stoichiometry occurring in the surface mixed layer,
subtropical gyre regions also exhibit anomalous apparent oxygen utilization (AOU) to nitrate
(NO₃⁻) stoichiometry in the shallow subsurface immediately below the euphotic zone, which are
referred to in the literature as negative preformed nitrate (preNO₃⁻) anomalies between ~120 m to
65 180 m across the ocean subtropics (e.g. Emerson & Hayward, 1995; Johnson et al., 2010;
Fawcett et al., 2018; Letscher & Villareal, 2018; Smyth & Letscher, 2023). These anomalies arise
from the accumulation of dissolved nitrate within the shallow thermocline that is insufficient to
balance the apparent oxygen utilization coupled with expected O₂:N stoichiometry of marine
organic matter remineralization. Currently, there is a significant gap in our understanding of the
70 coupled C, N, and O₂ fluxes and their associated stoichiometries for the subtropical ocean.

The cycling of low-N organic matter (C:N > Redfield ratio of 6.6:1) is a candidate
process that may explain the observed seasonal drawdown of DIC in the surface mixed layer and
the subsequent seasonal nitrate/oxygen anomalies in the shallow thermocline as its production in
surface waters requires lower supplies of N and in turn, its remineralization at depth releases less
75 N than expected from AOU. Marine dissolved organic matter (DOM) upper ocean C:N
stoichiometries range from ~13:1 to 16:1 (Liang et al., 2023). Its consumption in the shallow
thermocline of the subtropical gyres has been linked to explaining a portion of observed negative
preNO₃⁻ anomalies (Abell et al., 2005; Letscher and Villareal, 2018). However, residual preNO₃⁻
anomalies (positive in the lower euphotic zone, i.e. O₂ production without a balanced N supply;
80 negative in the shallow thermocline, i.e. O₂ consumption without balanced N release) still exist
after accounting for this process at both the BATS and HOT time series sites (Letscher and
Villareal, 2018), suggesting contributions from additional biogeochemical fluxes operating at
more extreme non-Redfield C:N:O₂ stoichiometries. The cycling of high C:N ratio marine gels
such as exopolymers TEP (transparent exopolymer particles) and CSP (Coomassie stainable



85 particles) between the mixed layer and the shallow thermocline has been implicated as an additional low N organic matter pool that can help explain the coupled C:N:O₂ anomalies across depths (Curran et al., 2025; Fawcett et al., 2018; Letscher and Villareal, 2018).

Both TEP, comprised of acidic polysaccharides (Azetsu-Scott and Passow, 2004), and protein containing CSP (Thornton, 2018), exhibit low N content, with estimates of marine gel
90 C:N stoichiometry ranging from ~16:1 to ~34:1 (Curran et al., 2025). The cycling of TEP and CSP, could help explain DIC drawdown within the surface layer with little requirements for additional nutrient sources delivered to the mixed layer. In addition, the oxygen consumed to remineralize exopolymers does not yield the N in the shallow thermocline that is expected from Redfieldian organic matter or moderately elevated DOM C:N:O₂ stoichiometry (Liang et al.,
95 2023) potentially explaining the negative ‘preformed’ nitrate anomaly found immediately below the euphotic zone within the subtropical ocean gyres.

While recent studies have begun to better quantify the abundance of marine exopolymers across the subtropics (e.g., Cisternas-Novoa et al., 2015; Curran et al., 2025; Kodama et al., 2014; Tian et al., 2025; Wurl et al., 2011), there is limited data on upper ocean rates of TEP and
100 CSP formation and consumption. In this paper, we report TEP and CSP formation and remineralization rates within the North Pacific subtropical gyre (NPSG) from surface and subsurface incubations performed at two stations in June 2021. We then examine the potential contribution of these processes to the seasonal ‘preformed’ nitrate anomalies. The main goals of this study are: (1) assess the rates of production and remineralization of TEP and CSP in surface
105 (5 m) and subsurface (125 m) waters; (2) determine the C:N, O₂:C, and O₂:N stoichiometry of TEP and CSP formation and remineralization; and (3) investigate the possible differences in net TEP production and remineralization fluxes across spatial and depth gradients within the subtropical gyre.

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2. Methods

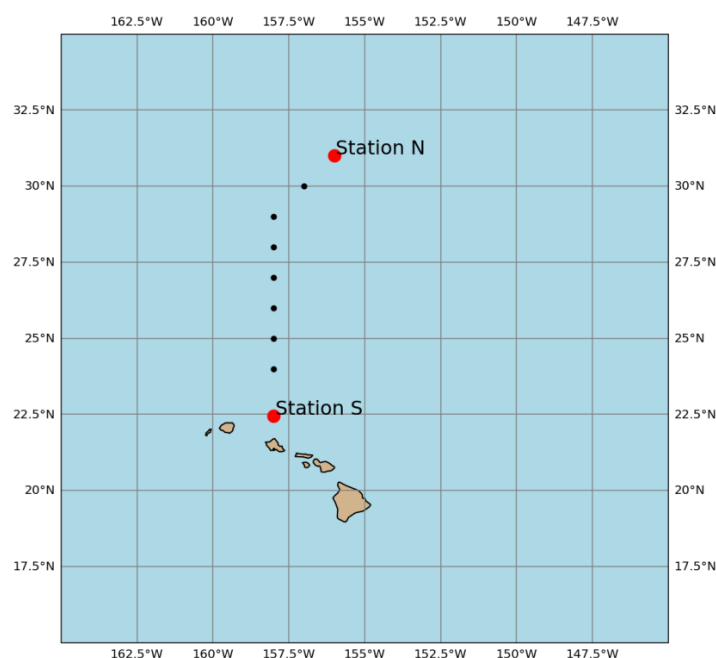


Figure 1: Map showing the location of the incubation experiments performed in June 2021. The cruise transects between station ALOHA (22.75° N, 158° W; Station S) and 31° N, 156°W; Station N. Experiments were done at 5 m and 125 m at each station.

2.1 Incubation Experiments

To study TEP and CSP exopolymer formation and consumption rates, seawater samples were collected from two stations during a 12-day cruise in June 2021, following a meridional transect from 22°45'N to 31°N (Fig. 1). Seawater incubations were conducted at Station ALOHA (22°75'N, Station S) and at 31°N (Station N). At these two stations, water was taken at 5 m within the mixed layer and at 125 m, just below the deep chlorophyll maximum (Experiments S(5m), N(5m), S(125m), N(125m)). At each station and depth, approximately 100 liters of seawater were collected via Niskin bottles mounted on a CTD/Rosette and placed in two 50 L HDPE acid-washed and rinsed carboys (Nalgene®). The following treatments were conducted in triplicate by placing 10L of initial volume into acid-cleaned and rinsed 10 L HDPE amber carboys (Justrite®): (1) Whole water (W), 100% seawater; (2) Filtrate (F), 100% 0.2 µm-filtered water; and (3) Mixed (M), 80% filtrate and 20% whole water, i.e. a grazer dilution culture



130 experiment. For the F and M treatments, gravity filtration was used through an in-line Pall
Acropak 1000 (0.8/0.2 μm) filter attached directly to the 50 L carboy spigot with silicone tubing.
The mixed (M) treatment is a dilution culture experiment, which aims to relieve microbial
heterotrophs from grazing pressure, allowing observation of bacterial consumption of organic
matter over the course of days (Carlson et al., 2002, 2004). The incubation carboys were then
135 stored in the dark within two deckboard environmental chambers maintained at the in situ
temperatures by use of recirculating surface or chilled (closed loop) seawater. The experiments
were performed over a period of 80-100 hours and samples were taken to measure exopolymer
formation or consumption, along with additional parameters such as enzyme assays and
respiration measurements. Experiments S(5m), S(125m), and N(125m) were sampled at 4
140 discrete time points, and Experiment N(5m) at 3 time points, after the incubation initiation,
spaced at ~ 1 -1.5 day intervals.

2.2 Exopolymer Concentrations

2.2.1 TEP and CSP measurements

TEP and CSP concentrations were determined spectrophotometrically following the
145 protocols of Bittar et al., (2018) for TEP and Cisternas-Nova et al.,(2015) for CSP with minor
modifications. TEP and CSP particles were collected by filtering 1 L of experimental water for
each exopolymer concentration measurement onto a 25 mm diameter, 0.4 μm polycarbonate
filter (Whatman) using a Masterflex ® peristaltic pump with Masterflex silicone tubing. The
filters were then transferred to a polycarbonate filter tower, where TEP sample filters were dyed
150 with an acidified (pH 2.5) 0.02% Alcian Blue dye solution (Alcian Blue 8X, Sigma Aldrich) and
CSP filter samples with a 0.04% Coomassie Brilliant Blue dye solution (SERVA) at pH 7.4. The
stained filters were then kept in the -20°C freezer until they were shipped back to the land-based
laboratory for analysis. TEP samples were extracted with 80% sulfuric acid. CSP samples were
extracted using 3% sodium dodecyl sulphate (SDS) in 50% isopropyl alcohol solution. Alcian
155 Blue absorbance is measured at 787 nm and Coomassie Blue at 615 nm. The standards were
created by measuring the absorbance of a dilution series of xanthan gum (XG) (Sigma) for TEP
and bovine serum albumin (BSA) (Sigma) for CSP. The concentrations of TEP and CSP achieved
through these measurements are quantified in units of $\mu\text{g L}^{-1}$ in xanthan equivalents ($[\text{xg-}$
 $\text{eq./L}]$)_and $\mu\text{g L}^{-1}$ in bovine serum albumin equivalents ($[\text{bsa-eq./L}]$), preceding any subsequent



160 conversions. TEP sample replicates had a mean variation coefficient of 0.04 and CSP samples 0.14 (n=24) from 8 sets of triplicate measurements (Curran et al., 2025).

2.2.2 Exopolymer concentration conversions

Measured TEP [xg-eq./L], was converted to carbon units using the conversion factor modified by Engel & Passow (2001) to [$\mu\text{M C}$]. Measured CSP [bsa-eq./L], was converted to
165 nitrogen units using the conversion factor modified by Engel & Passow (2001) to [$\mu\text{M N}$]. The modified C and N conversion factors were previously estimated empirically at the nearby Station ALOHA by Curran et al., (2025) . Mean values from Curran et al.,2025 were used as 0.625 for the carbon conversion factor and 0.005 for the nitrogen conversion factor.

$$\text{Carbon conversion factor} = \frac{\mu\text{M Exopolymer Carbon}}{\mu\text{g XG equiv L}^{-1}} \quad (1)$$

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$$\text{Nitrogen conversion factor} = \frac{\mu\text{M Exopolymer Nitrogen}}{\mu\text{g BSA equiv L}^{-1}}$$

2.3 Respiration (INT) Calculation

The 2-para (iodophenyl)-3(nitrophenyl)-5(phenyl) tetrazolium chloride (INT) reduction proxy assay of García-Martín et al., (2019) was implemented to quantify the respiratory activity within the incubated water. INT reduction to its reduced form, formazan (INTf), is used as a
175 proxy for the respiratory activity of plankton cells (García-Martín et al., 2019). At each incubation time point, incubation water was subsampled and analyzed following the García-Martín et al., (2019) method. The INT reagent was added to the sample and placed in the incubation tank for 1.5 hours and then placed in a -20°C freezer for later laboratory analysis.

Once samples were at the UNH laboratory, propanol was added to each sample and heated
180 up for 30 minutes at 50° C in an ultrasonic bath. The samples were then vortexed, transferred to centrifuge tubes, and centrifuged for ten minutes. Samples were then added to acrylic 1 cm pathlength cuvettes and run on a Shimadzu UV-Vis spectrophotometer to measure the absorbance at 485 nm. The absorbance was converted to community cellular respiration rates using:

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$$\log\text{CR}_{\text{O}_2} = 0.72\log\text{INT}_R + 0.44 \quad (2)$$



which is an empirical relationship fit to data collected from the Atlantic and Pacific Oceans including specifically the NPSG. CR_{O_2} provides a rate estimate on the change in O_2 in the incubated water due to community respiration of organic matter. In this work, we sought to quantify the stoichiometry of C:N, O_2 :C, and O_2 :N ratios for TEP-C and CSP-N remineralization. To calculate the delta $[O_2]$ concentration change during remineralization (treatments with negative TEP-C and CSP-N vs time slopes). INT rates ($nM O_2/h$) were time integrated following Equation 3.

$$\int_{t_1}^{t_2} INT dt = nM \Delta O_2 \quad (3)$$

The delta O_2 concentrations of remineralization were then converted to μM so that the values can be directly compared to TEP-C and CSP-N when quantifying the stoichiometry.

2.4 Exopolymer Production and Consumption Rates

TEP and CSP net consumption rates were estimated by calculating the slope during time intervals when the $[TEP]$ or $[CSP]$ vs time slope is negative ($\frac{-\Delta TEP/CSP}{\Delta Time}$) for the whole and mixed treatments. The mean and standard error of the mean (SEM) of all the negative slopes for all whole and mixed water treatments for each experiment are reported in Table 1. TEP and CSP production rates were calculated by isolating the time intervals when the slope of $[TEP]$ or $[CSP]$ were positive ($\frac{\Delta TEP/CSP}{\Delta Time}$) in the filtrate treatments, where net exopolymer production (ingrowth) dominates following prior filtering out of all marine particles. The mean of all positive slopes was calculated along with the standard error for each experiment.

3. Results

3.1 Incubation exopolymer and oxygen variability

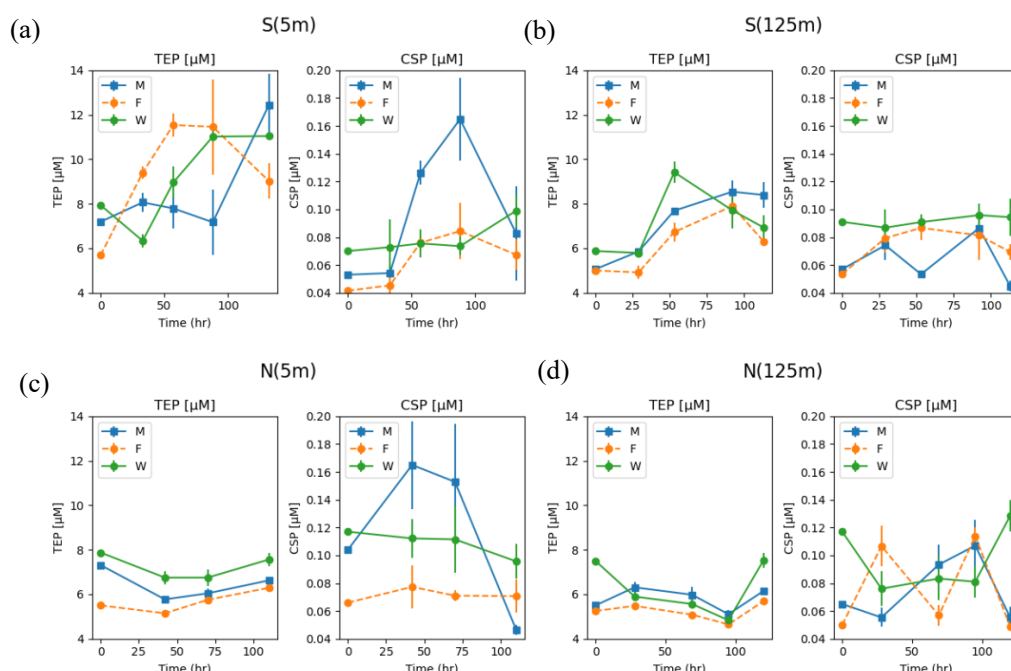


Figure 2: Means and standard error of [TEP] (μM) and [CSP] (μM) vs incubation time (h), of the following SW incubation experiments (A.) Station ALOHA- S(5m), B.) Station ALOHA- S(125m), C.) 31°N – N(5m), D.) 31°N – N(125m). Mixed treatment (M) in the blue line with square markers, whole treatment (W) green line with circle marker, and filtrate treatment (F) orange dashed line with circle marker.

TEP and CSP concentrations ($\mu\text{M C}$ and $\mu\text{M N}$, respectively) over the time course of each incubation experiment are shown in Figure 2, ranging from $\sim 5 - 12 \mu\text{M C}$ and $\sim 0.04 - 0.16 \mu\text{M N}$. TEP concentrations within the south station (S(5m), S(125m)) generally increased over the experiments (50h-120h), consistent across the Whole, Filtrate, and Mixed treatments, with maximum concentrations ranging from 9.4 to $12.4 \mu\text{M C}$ (Fig. 2, a, b). In contrast, at the northern station (N(5m), N(125m)) TEP concentration experienced modest increases/decreases to no change throughout the experiments, with TEP concentrations ranging from 4.6 to $7.9 \mu\text{M C}$ (Fig. 2, c,d). The CSP concentrations in the 5m Mixed experiments and both stations (S(5m), N(5m)) increased by $\sim 50\%$ N(5m) or $\sim 300\%$ S(5m) until 75 h, then declined. The CSP concentrations at 125m at both stations did not increase in the Mixed treatments and overall were less variable (Fig. 2, b,d). Within the Filtrate treatments, across stations and depths, both TEP and CSP were observed to increase between initiation and $\sim 75 - 100$ h, with the exception of the



N(125m) experiment. There was no correlation between TEP and CSP consumption or production rates throughout the incubations (Text S3). This decoupling of the TEP/CSP pools suggests possibly different roles within the exopolymer pool.

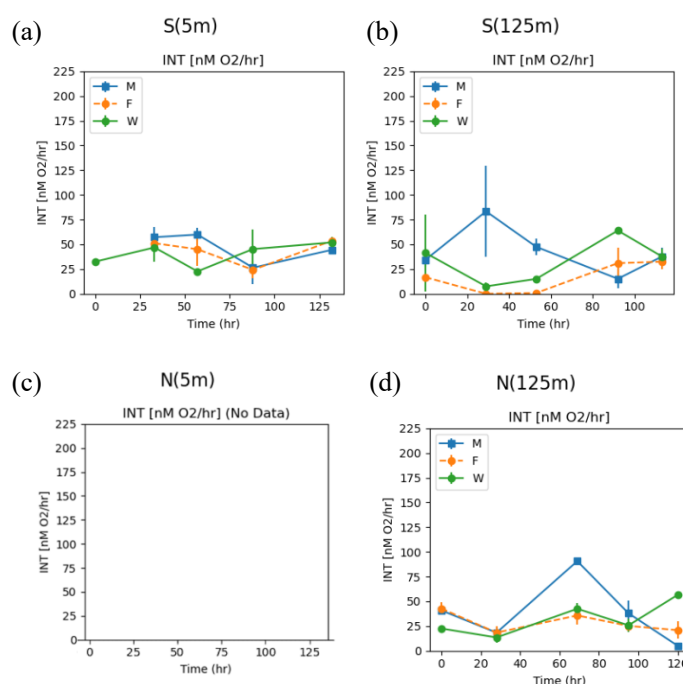


Figure 3. INT (nM O₂/h) activity of the following SW incubation experiments (A.) Station ALOHA- S(5m), B.) Station ALOHA- S(125m), C.) 31° N – N(5m), D.) 31° N – N(125m) with calculated standard error for the triplicate incubations represented in the error bars. Mixed treatment (M) in the blue line with square markers, whole treatment (W) green line with circle marker, and filtrate treatment (F) orange dashed line with circle marker.

INT reduction assays were performed as a proxy for community respiration rates, which has been converted to O₂ consumption units (Equation 3). The Mixed treatments in each of the experiments with INT data—S(5m), S(125m), and N(125m)—showed a slightly elevated O₂ consumption rate relative to the Filtrate and Whole treatments, with the maximum rates ranging from 59.9 to 90.7 nM O₂/hour (Fig.3). There are observably higher elevated INT rates (when grouping the M & W treatments) in the Northern stations compared to the Southern stations, although not statistically significant (Welch t-test; p-value of 0.13). The Filtrate and Whole water treatments exhibited slightly lower rates, with the maximum change in O₂ ranging from



32.5 to 53.6 nM O₂/hour (Fig.3). We were unfortunately unable to get N(5m) INT data due to
245 methodological issues.

We examined the potential relationship between INT as a proxy for respiration and TEP
and CSP consumption rates (pooling the M & W treatments) throughout the incubations
expecting to see a positive relationship between respiration and gel consumption rates. Within
the TEP pool, there was a stronger relationship with INT at depth, e.g., S(125 m) and N(125m)
250 had higher correlations but remained statistically not significant, at the 95% confidence interval.
S(125 m) showed a strong positive association (Kendall $\tau = 1.0$, p value = 0.08, n=4), whereas
N(125 m) showed a strong negative association (Kendall $\tau = -0.73$, p = 0.07, n= 5). Within the
surface incubation, S(5 m), there was a negative weak to moderate association between TEP
consumption rates and INT rates (Kendall $\tau = -0.33$, n=3), which was again not statistically
255 supported (p value = 1.0), which is consistent with evidence of net TEP accumulation at S(5m).
As for CSP, we did not detect evidence of an association between CSP consumption rates and
INT in the Southern station experiments. While N(125 m) showed a moderately strong positive
association (Kendall $\tau = 1.0$, p = 0.08, n= 4).

We measured α -glucosidase throughout the incubations, GLUC-ASE (nM C/h) activity
260 (Fig. S1) which measures the potential community activity of α -glucosidase, an enzyme used to
break down polysaccharides, which we hypothesized could serve as a proxy for exopolymer
degradation. We found no clear relationship between glucosidase activity as a proxy for
polysaccharide degradation and TEP consumption rates (grouping the M&W treatments)
throughout the incubations (Text S1, Text S2). We did find the southern stations having elevated
265 rates of activity compared to the northern experiments, with a p-value of 0.012 (Welch t-test).
We also observed elevated rates of glucosidase activity in the upper 5 m compared to the
incubations at 125m depth when both stations are pooled, with a p-value of 0.05 (Welch t-test).

3.2 Exopolymer Formation and Consumption Rates

Table 1. Exopolymer Mean Formation Rates (nM/h), standard error of the mean (SEM), and
270 number of instances (n) as calculated from the Filtrate treatments.



Station	Mean TEP production (nM C/h)	SEM	n	Mean CSP Production (nM N/h)	SEM	n
S(5m)	100.9	11.5	2	0.55	0.36	3
S(125m)	52.7	22.8	2	0.60	0.29	2
N(5m)	17.6	4.0	2	0.27	N/A	1
N(125m)	24.9	16.7	2	2.11	0.08	2

Table 2. Exopolymer Mean Consumption Rates (nM/h), standard error of the mean, and number of instances (n) as calculated from the Whole and Mixed treatments.

Station	Mean TEP consumption (nM C/h)	SEM	n	Mean CSP Consumption (nM N/h)	SEM	n
S(5m)	-26.7	11.3	3	-0.96	0.90	2
S(125m)	-22.6	10.3	4	-0.77	0.44	4
N(5m)	-31.8	5.0	2	-0.73	0.49	5
N(125m)	-20.9	12.8	2	-1.21	0.86	2

*For N(125m) removing the whole treatment.

275 Mean TEP and CSP formation rates (nM C/h and nM N/h) as gauged from TEP and CSP concentration increases within experimental time course of the Filtrate treatments are shown in Table 1. Mean TEP formation rates at the South Station (100.9-52.7 nM C/h), are higher (Welch t-test; p-value 0.04) compared to the North Station (25.9 – 17.5 nM C/h) (Table 1). Mean TEP and CSP consumption rates (nM C/h and nM N/h) as gauged from TEP and CSP concentration decreases within the Whole and Mixed treatments are shown in Table 2. TEP consumption rates exhibited minimal differences between stations and depths (Table 2). TEP consumption rates were slightly higher at the center of the gyre (27.1 – 31.7 nmol C/h; North Station) than at the South Station (22.6 – 26.7 nmol C/h) (Table 2), although not statistically significant (Welch t-test; p-value 0.84). Within the Filtrate treatment, TEP and CSP production rates are 1.3 to 4.3 times larger than the respective consumption rate for each depth and station (Table S1), suggesting that the filtrate treatment largely tracks the exopolymer production rates for each

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experimental location. The Filtrate treatments are initiated with 0.2 μm filtered seawater, which removes all exopolymers included along with all other particulates in the media, allowing ingrowth of gels from DOM precursors over the time course of the experiments (Curran et al., 2025; Verdugo, 2021).

CSP cycling rates were primarily dominated by consumption over production when comparing rates of each within a station and depth, except for 125m at the North Station, with a mean net consumption rate of -0.35 nM N/h (Table 1). There is no significant difference between CSP production rates across latitudes (Welch t-test; p-value 0.26). However, when comparing CSP rates between surface (5m) and (125m) there was a significantly higher rate of production at depth (125m, $0.60\text{--}2.11 \text{ nM N/h}$) compared to the surface (5m, $0.27\text{--}0.55 \text{ nM N/h}$) (Table 1) with a p-value 0.006. Mean CSP consumption rates are greater at the southern station (station ALOHA) with ($0.97\text{--}5.72 \text{ nM N/h}$) compared to ($0.73\text{--}0.99$; Northern Station), although there is no statistically significant difference (Welch t-test; p-value 0.95). CSP had slightly higher consumption rates at depth compared to the surface, with 125 m having rates ranging from ($0.99\text{--}5.72 \text{ nM N/h}$) and ($0.73\text{--}0.97 \text{ nM N/h}$) at 5 m (Table 2) although not statistically significant (Welch t-test; p-value 0.719). CSP rates were more consistent station-to station, where TEP cycling rates exhibited more variability station-to-station.

3.3 Exopolymer Remineralization Stoichiometry

Table 3. Mean exopolymer $\text{O}_2\text{:C}$, $\text{O}_2\text{:N}$, and C:N remineralization stoichiometry, standard error of the mean, and number of instances (n), estimated from the incubation experiments.

Station	$\text{O}_2\text{:C}$	SEM	n	$\text{O}_2\text{:N}$	SEM	n
S(5m)	3.9	0.9	5	59.8	28.9	2
S(125m)	1.3	0.2	6	65.1	6.9	4
N(5m)	N/A	N/A	N/A	N/A	N/A	N/A
N(125)	2.8	0.4	4	31.8	7.8	4

*For N(125m) removing the whole treatment.

Overall Mean $\text{O}_2\text{:C}$	SEM	Overall Mean $\text{O}_2\text{:N}$	SEM	Overall Mean C:N	SEM
2.7	0.6	52.3	13.5	19.4	0.4

*For N(125m) removing the whole treatment.



Delta [O₂], [TEP-C], and [CSP-N] changes for observed declines in TEP and CSP are
310 shown in Table 3 along with the mean derived exopolymer remineralization stoichiometry. The
mean exopolymer remineralization ratios all deviated from the canonical Redfield ratio observed
in marine plankton and suspended particulate organic matter. The calculated O₂:C, 1.3:1 to 3.9:1,
are similar to or up to two-fold higher than the Redfield ratio of (O₂:C = 1.3: 1). The O₂:N also
follows a similar trend, greatly diverging from the Redfield ratio of (O₂:N = 8.6:1) with a range
315 of ~32:1 to 65:1, where a much larger fraction of O₂ is being utilized compared to nitrogen
released (Table 3). The overall mean C:N ratio for exopolymer remineralization, computed from
the empirically estimated O₂:N and O₂:C stoichiometries is elevated (19.4:1) compared to
Redfield (6.6:1), and DOC:DON (~7-10:1) (Letscher and Moore, 2015).

To justify our assumption that the net oxygen consumption gauged by the time
320 integration of the INT rates in the incubations is capturing TEP, we quantified any net TOC
consumption over the course of the experiments (Fig S3). Using the O₂:C stoichiometry of POC
(1.3:1) and DOC (1.6:1) consumption in the study area, we deduce an O₂:TOC stoichiometry of
1.4:1. We then multiplied the change in TOC by this O₂:TOC factor (1.4) during periods when
TOC was decreasing, signifying remineralization (Text S4), to obtain the contribution of TOC
325 remineralization to total respiration. We then estimated the gel contribution by finding the
difference in INT and O₂ remineralization due to TOC during intervals when both TOC and TEP
were decreasing.

Additionally, we examined NO₃⁻ and PO₄³⁻ concentration variability within the
incubations to identify possible instances of DON and DOP remineralization, which should
330 manifest as net accumulations of inorganic nutrients. This occurred only in the incubation at
Station N (125 m) for the Whole treatment (Fig. S4). Data from that treatment were excluded
from the calculation of exopolymer remineralization stoichiometry to ensure that we isolated
TEP and CSP consumption and their corresponding stoichiometries.

4. Discussion

335 **4.1 TEP and CSP distributions and rates of consumption and formation across depths
and stations**

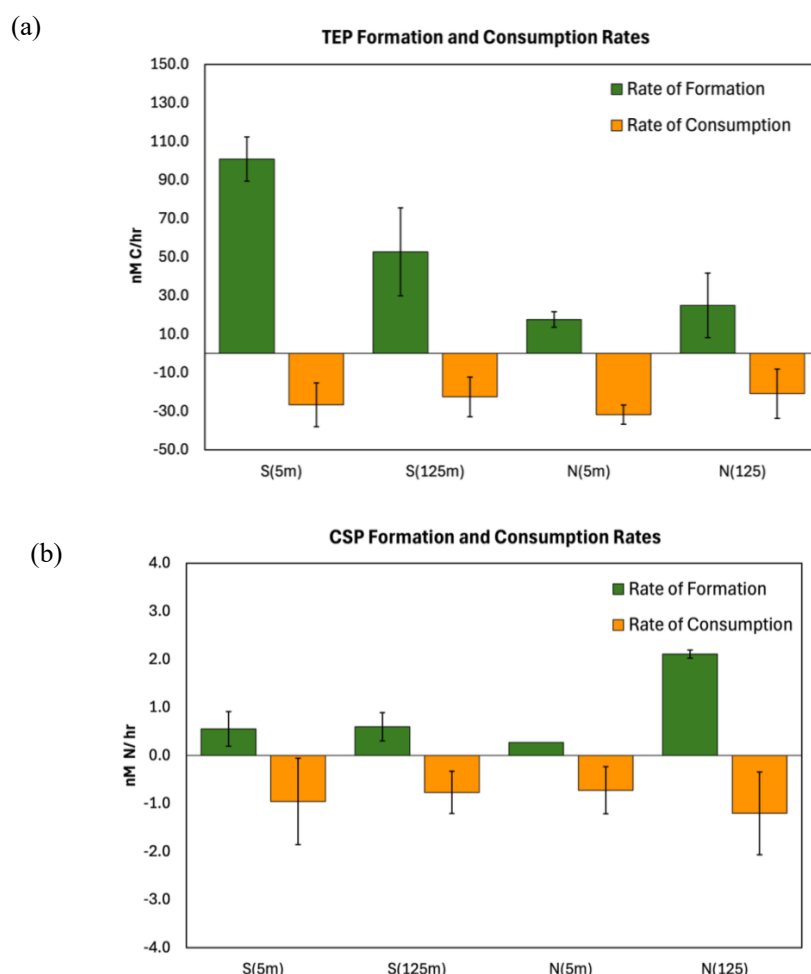


Figure 4: Bar graph representation of the data in Tables 1 and 2 comparing TEP and CSP formation and consumption rates across experiments and stations. Error bars represent the SEM. A.) The average rate of TEP formation (nM C/h) from the Filtrate treatment in green; average rate of TEP consumption (nM C/h) from the Mixed and Whole treatments. B.) Shows the average rate of CSP formation (nM N/h) in green and CSP consumption (nM N/h) in orange.

Marine gels such as TEP and CSP are ubiquitous within the world's surface oceans, with abundances around 10^6L^{-1} and slightly higher abundances (10^8L^{-1}) observed within phytoplankton blooms (Cisternas-Novoa et al., 2015). Phytoplankton have been shown to produce the dissolved precursors to both TEP and CSP, making it common for TEP and CSP to be studied in parallel to one another. Within this study, the cycling of TEP and CSP throughout the incubations did not correlate (Fig. 4). These differences within the incubations suggest these



parts of the exopolymer pool may cycle differently. TEP production rates are 4 times faster than consumption rates at S(5m) compared to CSP, which experiences greater accumulation at N(125) (Fig. 4).

This divergence in marine exopolymer behavior is observed via differences in TEP and CSP concentrations throughout the incubations. At Station ALOHA, TEP concentrations were notably higher (Fig. 2 a,b), accompanied by elevated TEP production rates (Fig. 4a). The increased production at the southern station exceeded TEP consumption at both depths (5 m and 125 m), indicating a net accumulation of TEP at Station ALOHA during this time of year (Fig. 4a). Whereas, towards the center of the gyre, at 31°N, there is an increased rate of TEP consumption, which exceeds production at 5m and is equivalent to production at 125m, suggesting no accumulation of TEP(Fig. 4a.).

Net accumulation of TEP within the mixed layer, particularly at station ALOHA (S(5m), Fig. 4a) accompanied by elevated O₂:C and C:N ratios of its consumption (Table 3) can provide explanations for preformed NO₃⁻ anomalies observed in the subsurface, should the gel pool be exported to depth via either slow gravitational settling or vertical mixing of the water column (Abell et al., 2005; Letscher and Villareal, 2018; Smyth and Letscher, 2023; Toggweiler, 1993). CSP concentrations exhibit reduced variability across stations and depths, with a slightly depressed CSP concentration at S(125m), which is the station with the highest consumption rate of CSP across the experiments (Fig. 4b). All stations and depths suggest a balanced to net remineralization of CSP-N, with the exception at 125 m at 31°N where there was evidence of net production (Fig. 4b).

4.2 Remineralization Stoichiometry

Understanding the elemental stoichiometry of these exopolymers is important for assessing how this organic matter pool may explain observed dissolved inorganic carbon and preformed nitrate anomalies and if they complete the associated elemental budgets for the ocean subtropics (Letscher and Villareal, 2018). While the Redfield ratio represents a global average of C, N, P, O₂ (106:16:1:138) for marine plankton and suspended particulate organic matter, localized stoichiometric variations can deviate significantly from this standard (e.g. Martiny et al., 2013). These deviations offer valuable insights into regional biological pump dynamics and ocean productivity.



Previous studies have operated with an assumption of 1:1 O_2 : C stoichiometry when discussing TEP cycling (e.g. Curran et al., 2025; Fawcett et al., 2018; Letscher & Villareal, 2018). This assumption was based on a simple carbohydrate stoichiometry, as TEP primarily contains carbohydrate material. In our study, we found an exopolymer pool stoichiometry of
385 2.7:1 O_2 :C (Table 3), which suggests more oxygen is required to remineralize gels than previously assumed.

The elevated exopolymer elemental stoichiometry of the O_2 :N ratio can provide insight into TEP and CSP being a contributing mechanism to the observed $PreNO_3^-$ negative anomalies in the region. A mean calculated (O_2 : CSP-N) of 52.1: 1 (Table 3), indicates that the
390 remineralization of CSP-N has a greater demand for oxygen relative to nitrogen release. This suggests that the subsequent export of slow-sinking and/or vertically mixed TEP and CSP and their remineralization with elevated O_2 :N ratios can be a mechanism whereby O_2 is consumed without the appreciable production of NO_3^- within shallow mesopelagic depths. The calculated O_2 :N stoichiometry of the gel pool is far outside the norm compared to other organic matter
395 pools. When observing marine organic matter stoichiometry, the Redfield ratio has a O_2 :N of ~8.6 (138/16, Redfield, 1934). When differentiating between the organic matter pools, the NPSG DOM calculated by Letscher & Villareal, (2018) is ~18:1 and the calculated POM remineralization stoichiometry ranges from ~8-10:1 in the upper 200m (Gerace et al., 2023; Letscher and Villareal, 2018). The two dominant fractions of the total organic matter pool; the
400 DOM and the POM have O_2 :N stoichiometries much lower than the observed O_2 :N stoichiometry of the gel pool. The elevated O_2 :N ratio calculated from the remineralization of the gels is greater evidence that the exopolymer fraction of the total organic matter pool can contribute to the negative preformed nitrate anomalies within the subsurface because there is little nitrogen released under a large oxygen utilization.

405 This study calculated exopolymer elemental remineralization stoichiometry (Table 3), rich in C and depleted in N ($C:N = 19.4$) present in June within the surface ocean in the NPSG. The standing stock of the exopolymer pool in June reported in Curran et al., (2025) had a C:N stoichiometry of ~26-38:1; the remineralization stoichiometry reported here of 19.4 is lower. A remineralization C:N stoichiometry lower than that of the standing stock provides evidence of
410 preferential remineralization of nitrogen from the gels relative to carbon, which is consistent with



the higher rates of CSP consumption over TEP across the stations and depths investigated (Fig. 4). Coupled with the highest rates of TEP accumulation at Station S (Fig.4a) emphasizes the southern edge to be accumulating gel organic carbon in the surface ocean during the early summer.

415 **4.3 Preformed NO_3^- anomalies within the NPSG**

The summertime DIC drawdown in the mixed layer in the absence of measurable NO_3^- is a persistent feature of the NPSG which has thus far eluded a complete accounting of the N sources required to balance C export (e.g. [Curran et al., 2025](#); [Johnson et al., 2010](#); [Keeling et al., 2004](#)). Biogeochemical Argo floats have detected near-monthly episodic events (presumably
420 eddies) that transport ‘new’ nutrients upward from depth, supporting NCP (Johnson et al., 2010). However, these physical forcings only reach shallowest depths of approximately 75 m and cannot fully account for the observed DIC drawdown occurring in the surface mixed layer (upper ~40 m) and the nitrate deficit, quantified as a negative preformed NO_3^- anomaly at ~120-180 m (Johnson et al., 2010; Letscher and Villareal, 2018). Lateral mixing of both inorganic and organic
425 nutrients towards the NPSG also plays a role in closing the nutrient budget (Letscher et al., 2016) but preferentially fertilizes the lower depths of the euphotic zone. As physical mixing processes fall short of explaining this anomaly (Johnson et al., 2010; Letscher et al., 2016) Letscher & Villareal, (2018) and Fawcett et al., (2018) proposed three additional candidate biogeochemical mechanisms to close the C, N, and O_2 budgets: (1) vertically migrating phytoplankton, (2)
430 vertically separated production and (3) remineralization of TEP, and (4) bacterial heterotrophic NO_3^- consumption.

TEP and CSP gels often aggregate into marine snow, which has been shown to transport organic matter into the ocean interior (Passow, 2002). Although TEP and CSP themselves are naturally positively buoyant (Mari et al., 2017), the addition of ballast materials—such as
435 lithogenic particles—can increase aggregate density ($1.04\text{--}1.12\text{ g cm}^{-3}$; Mari et al., 2017). This ballasting effect allows some fraction of the TEP/CSP pool to become negatively buoyant and sink slowly through the water column, thereby contributing to carbon export and influencing oxygen budgets (Mari et al., 2017). Alternatively, a non-mutually exclusive process for exporting the exopolymer pool below the euphotic zone can occur via seasonal convective overturn of the
440 upper ocean which is important for exporting DOM (Hansell and Carlson, 2001) and suspended



POM (Dall’Olmo et al., 2016). The importance of this process increases poleward, coinciding with where we see net consumption of TEP/CSP at depth (e.g. at 31°N in Fig. 4). This suggests that the consumption of these carbon-rich and nitrogen-poor gels below the euphotic zone could be a mechanism to explain a portion of the residual preformed nitrate anomaly.

445 We aim to estimate the contribution of vertically separated marine gels’ (TEP/CSP) cycling as contributing towards the negative preformed NO_3^- anomaly in the subsurface across the southern latitudes of the NPSG. Through surface and depth incubations, we derived the non-Redfieldian stoichiometry of TEP/CSP remineralization, which was missing from the calculations by Letscher & Villareal, (2018). Their work suggested that TEP cycling contributes
450 to both positive and negative preformed NO_3^- anomalies within the lower euphotic zone and shallow mesopelagic, respectively at Station ALOHA. Our findings allow for a revised C:N and O_2 :N stoichiometry of remineralization for the marine gel pool to be applied, providing a more accurate assessment of the extent of TEP/CSP contributions to preformed NO_3^- anomalies within the NPSG. Furthermore, we propose a new formulation of PreNO_3^- (Preformed Nitrate tracer),
455 originally defined by Broecker, (1974) and later revised by Letscher & Villareal, (2018) as residual PreNO_3^- (rPreNO_3^-) to explicitly include contributions of DOM to apparent oxygen utilization (AOU), here to explicitly include the gel pool (TEP/CSP).

$$r\text{PreNO}_3^- = \text{NO}_3^- \text{ measured} - \left(f_{\text{DOM}} \cdot \frac{\text{AOU}}{r_{\text{DOM}}} \right) - \left(f_{\text{POM}} \cdot \frac{\text{AOU}}{r_{\text{POM}}} \right) - \left(f_{\text{GEL}} \cdot \frac{\text{AOU}}{r_{\text{GEL}}} \right) \quad (4)$$

For comparisons in this study, we will refer to the tracer as defined in Letscher & Villareal,
460 (2018) as preformed NO_3^- (Pre NO_3^-) (i.e. separate contributions to AOU from POM and DOM; see Text S5), and the updated equation will be defined as residual preformed NO_3^- (rPre NO_3^-) (i.e. separate contributions to AOU from POM, DOM, and gels; Equation 4).

Oxygen and nitrate data collected on nine unique stations across the June 2021 transect (Fig. 1) and reported in Curran et al., (2025) are used to calculate both PreNO_3^- and rPreNO_3^- across
465 the southern NPSG nominally along 158°W from Station ALOHA north to 31°N (Fig. 5) AOU was determined as the difference between oxygen saturation ($\text{O}_{2 \text{ sat}}$) and the measured oxygen ($\text{O}_{2 \text{ measured}}$). $\text{O}_{2 \text{ sat}}$ was calculated using the CTD temperature, salinity, and pressure via the ODV software (Schlitzer, n.d.) using the Weiss, (1970) algorithm. Values for f_{DOM} (0.5) and r_{DOM} (18.1) for the NPSG were taken from Letscher & Villareal, (2018), where f_{DOM} represents the



fraction of AOU attributable to DOM, and rDOM is the stoichiometric ratio of O₂ consumed per mole of DON remineralization. For the particulate matter (POM), rPOM was derived using the stoichiometric ratio of O₂ consumed per mole of PON, based on Paulmier et al., (2009), whose reported values ranged from 6.9 to 10.6. We adopted an intermediate rPOM value of 8.8, consistent with Anderson & Sarmiento, (1994) an updated stoichiometry from (Redfield, 1934).
Curran et al., 2025 determined fTEP values of 0.065 to 0.20 at station ALOHA, which were subsequently used to adjust fPOM to a range of 0.435–0.30. In this study, rGEL was calculated (Table 3) using gel O₂:N remineralization stoichiometry values of 59.8 and 65.1 obtained from Station ALOHA.

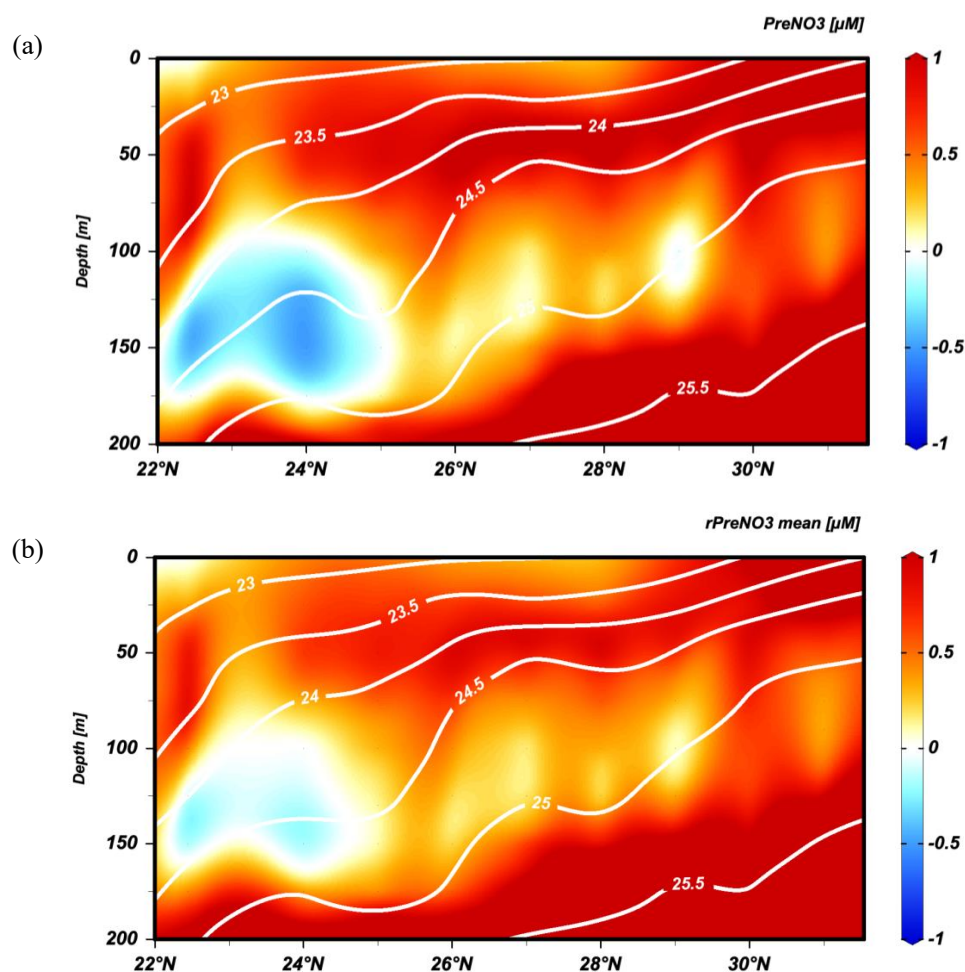




Figure 5: Meridional depth profiles of the June 2021 cruise transect (from 22.75 to 31° N along ~ 158° W) a.) the PreNO_3^- tracer [μM] as defined by Letscher & Villareal, (2018), b.) the revised rPreNO_3^- tracer [μM] (mean) with the consideration of the gel pool. The white contours are isopycnals of potential density anomalies, s_q [kg m^{-3}].

The further consideration of the gel pool operating under non-Redfieldian stoichiometries, as presented in Table 3, provides an additional mechanism to explain the PreNO_3^- anomalies observed in the NPSG. Incorporating the gel pool reveals an observable dampening of both the positive and negative preformed NO_3^- anomalies within the lower euphotic zone and shallow mesopelagic (Fig. 5).

To quantify the contributions that TEP/CSP have on the preformed NO_3^- anomalies within the NPSG, we took the difference between the PreNO_3^- tracer determined by Letscher & Villareal, (2018) and calculated rPreNO_3^- tracer determined by this study, then divided by preNO_3^- to get the percent contribution of the gel pool (Table 4, Text S6). In our incubations, we found relatively higher rates of gel activity at station S (5) and (125m), where we also found a greater gel contribution to the preformed NO_3^- anomaly throughout the transect (Fig S5) which could imply that the cycling of the marine exopolymer particle pool is a significant mechanism to partially explain these anomalies.

Table 4. TEP/CSP exopolymer (gel) contribution to the preformed NO_3^- anomalies

	Gel Contribution (%)	SEM	n
Overall	15.7	0.3	76
Positive pre NO_3^-	14.6	0.1	64
Negative pre NO_3^-	21.5	0.7	12

Overall, the surface ocean accumulation and subsequent vertical export and remineralization of the TEP/CSP gel pool can explain 15.7% of the observed PreNO_3^- anomalies on average (Table 4). The additional gel pool dampens the negative preformed NO_3^- anomaly present in the subsurface across the southern latitudes of the NPSG (Fig. 5,b) by 21.5% (Table 4). TEP/CSP contributes to dampening the positive preformed NO_3^- anomalies by 14.6% (Table 4). Working under the assumptions of 1:1 $\text{O}_2\text{:C}$ remineralization stoichiometry and C:N stoichiometry of the exopolymer pool of 25 ± 8 , Curran et al. (2025) estimated that the gel pool could potentially contribute 22-67% of the PreNO_3^- anomalies. Our results are consistent with the



lower bounds estimated by Curran et al (2025). Although more conservative, we were able to provide a more accurate estimate of the gel pool contribution within the NPSG PreNO_3^- anomalies of 14-22%, which accounts for the elevated $\text{O}_2:\text{C}$ and reduced $\text{C}:\text{N}$ remineralization stoichiometries diagnosed in this study from bioassay incubation experiments (Table 3). These results imply that the cycling of the marine exopolymer particle pool is a significant mechanism to explain the coupled $\text{C}:\text{N}:\text{O}_2$ anomalies present within the NPSG and should be considered as an additional pool when attempting to understand nutrient cycling and the associated carbon and oxygen budgets within subtropical surface oceans.

5 Conclusion

This study quantified rates of TEP and CSP formation and consumption inferred from incubation experiments within the surface ocean of the NPSG in June. TEP and CSP formation/consumption differed across latitude and depth, suggesting the TEP and CSP gel pools cycled independently and yielded contribution to rPreNO_3 that varied in time and space. We found evidence for net TEP accumulation at station ALOHA compared to 31°N and balanced to net consumption of CSP across stations and depths.

This accumulation of marine gels during the early summer (June 2021) is at a high $\text{C}:\text{N}$ stoichiometry, measured in our study at $\sim 26\text{--}38:1$ (Curran et al., 2025), higher than measured in Autumn at the same site and year, e.g. $17\text{--}19:1$. From the incubation experiments reported here, we estimate the $\text{C}:\text{N}$ stoichiometry for its consumption in June is lower, at ($\text{C}:\text{N} = 19.4$). This pattern suggests preferential remineralization of nitrogen over carbon within the gel pool is likely occurring during June in the NPSG, especially near Station ALOHA. We also found an elevated $\text{O}_2:\text{N}$ ratio ($52.3:1$) calculated from the remineralization of the gels, which suggests a much larger fraction of O_2 is being utilized than nitrogen being released. Elemental stoichiometries of organic matter in oligotrophic regions often vary substantially across space and depth (Letscher and Moore, 2015; Liang et al., 2023; Martiny et al., 2013), highlighting the need for region-specific measurements to accurately characterize local biogeochemical processes.

By quantifying non-Redfieldian remineralization stoichiometry of TEP/CSP cycling within the NPSG surface ocean, our analysis confirms the need to include TEP/CSP cycling to partially explain the presence of the PreNO_3^- anomalies within the ocean subtropics (e.g., Letscher & Villareal, (2018); Fawcett et al (2018)) and likely ‘unexplained’ summertime mixed layer DIC



drawdown as well (e.g. Johnson et al., 2010). However, our results suggest there is still room within the oxygen and nitrate budgets for important roles from the additional candidate processes, such as vertically migrating phytoplankton and bacterial heterotrophic NO_3^- consumption, which should be explored further to fully close the C, N, and O_2 budgets within the NPSG.

Data and Software accessibility

Incubation data was deposited in BCO-DMO <https://www.bco-dmo.org/project/772658>.

Transect data as reported in (Curran et al 2025) is available at <https://www.bco-dmo.org/dataset/968636>. All data are publicly available.

Author Contribution

RL and TV acquired the funding. KC and KZ preformed the measurements. SR analyzed the data and wrote the manuscript draft. RL, KC, KC, and KZ reviewed and edited the manuscript.

Conflict of Interest

The contact author has declared that none of the authors have a conflict of interest within this work.

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