

SAN FRANCISCO BAY
NUTRIENT MANAGEMENT STRATEGY

Carbon production and nitrogen drawdown of the
2022 *Heterosigma akashiwo* harmful algal bloom in
San Francisco Bay

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EXECUTIVE SUMMARY

In August 2022, San Francisco Bay (SFB) experienced an overgrowth of the raphidophyte *Heterosigma akashiwo*, resulting in the most extensive harmful algal bloom (HAB) on record. The progression of the bloom, and associated parameters including concentrations of dissolved oxygen (DO), chlorophyll *a* (chl *a*), and nitrate + nitrite (NO_x), were monitored using *in situ* high-frequency (15 min) moored sensors and boat-based high-speed surface mapping. The mooring data – with high temporal resolution – were used to estimate temporal changes in organic matter concentration ($\frac{dOC}{dt}$), while the mapping data – with high spatial resolution – were used for basin scale estimates of NO_x drawdown and chl *a* production. Both measurements show that substantial pre-bloom NO_x (25 μM) was fully converted to phytoplankton biomass, with peak bloom chl *a* levels > 100 μg L⁻¹. From the mooring data we identified three bloom phases tied to DIN supply: Phase 1 (rapid growth) – rapid increase in DO and chl *a* as DIN is drawn down to sensor detection limits; Phase 2 (slowed growth) – chl *a* slowly increases while DO decreases due to atmospheric transfer, Phase 3 (bloom collapse) – DO and chl *a* levels plummet, resulting in widespread hypoxia. $\frac{dOC}{dt}$ calculated for Phase 2 suggests that the bloom was sustained by ongoing DIN loading from publicly owned treatment works (POTWs), while close agreement between chl *a*- and DO-based $\frac{dOC}{dt}$ during Phase 3 suggests a top down pressure such as a marine virus likely precipitated the bloom collapse. Our results indicate that DIN loading from POTWs substantially contributed to the severity of the HAB, and support the need for upcoming load reductions.

Plain Language:

In August 2022, the San Francisco Bay experienced its worst harmful algae bloom on record. Nutrient Management Strategy scientists monitored the progression of the bloom with an array of moored sensors collecting water quality data every 15 minutes. In the South Bay, where the bloom was most pronounced, we conducted two additional mapping cruises during the bloom to gather data at a high spatial resolution.

We used the moored sensor data to estimate the bloom's net ecosystem metabolism, a useful metric that combines total production and respiration of an ecosystem during the event. The mapping data enabled us to estimate nutrient utilization and chlorophyll production at a basin-scale for the whole South Bay. From these analyses, we identified three phases of the bloom:

Phase 1 (Rapid growth) - Rapid growth of phytoplankton. Nutrients decrease, dissolved oxygen and chlorophyll sharply increase.

Phase 2 (Slowed growth) - Production nearly halts as nutrients are depleted. Chlorophyll continues increasing slowly and dissolved oxygen begins to decrease slightly as it transfers into the atmosphere.

Phase 3 (Bloom collapse) - Mass death of phytoplankton. Dissolved oxygen and chlorophyll levels plummet as phytoplankton die and decompose. The close alignment of dissolved oxygen and chlorophyll suggest the collapse may have been triggered by a marine virus.

Our findings suggest that nutrient loading from publicly owned treatment works substantially contributed to the severity of the bloom and support the need for upcoming load reductions.

Suggested citation:

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1. INTRODUCTION

Harmful algal blooms (HABs) have been increasing in prevalence globally over the past several decades (Gobler, 2020), imparting numerous deleterious impacts on coastal ecosystem health including direct toxicity to fauna and water column anoxia upon bloom collapse (Berdalet et al., 2016). During this same period coastal managers have increasingly utilized continuous high-frequency monitoring arrays to collect real-time values of key water quality parameters – including DO, chl *a*, and DIN –which act as early warnings for severe events including HABs (Bailey et al., 2019). These data provide key insight into HAB mechanics and ecosystem response, allowing for development of ecosystem metrics and the identification of drivers that describe HAB progression.

One key metric for understanding HAB mechanics is net ecosystem metabolism (NEM), defined as rate of change to the organic carbon (OC) pool of an ecosystem. In the case of HABs, NEM represents the integrated gain and loss of biological material over the course of an event. Real-time measurements of a changing NEM over the course of a HAB allow for insights into its underlying mechanisms, including biological, chemical, and physical drivers. Phytoplankton metabolism is often measured as the rate of change in dissolved oxygen (DO) using *ex situ* bottle incubations (Cole & Cloern, 1987; Regaudie-de-Gioux et al., 2023), or by empirical parameterizations based on chlorophyll *a* (chl *a*) and other environmental variables (Jassby et al., 2002). These techniques measure the metabolism of phytoplankton themselves, and do not capture the impacts of heterotrophic bacteria and other organisms on NEM. A semi-novel approach for calculating HAB NEM is to convert continuous scalar measurements from water quality sondes, such as DO, chl *a*, and dissolved inorganic nitrogen (DIN), to units of OC using stoichiometric ratios. This methodology is analogous to diel-open water methods often applied to DO data for estimating aquatic metabolism (Odum, 1956), with the main difference being that open-water estimates are typically separated and averaged by day (Staehr et al., 2010), whereas this approach uses multiple scalars and is applied over variable time periods.

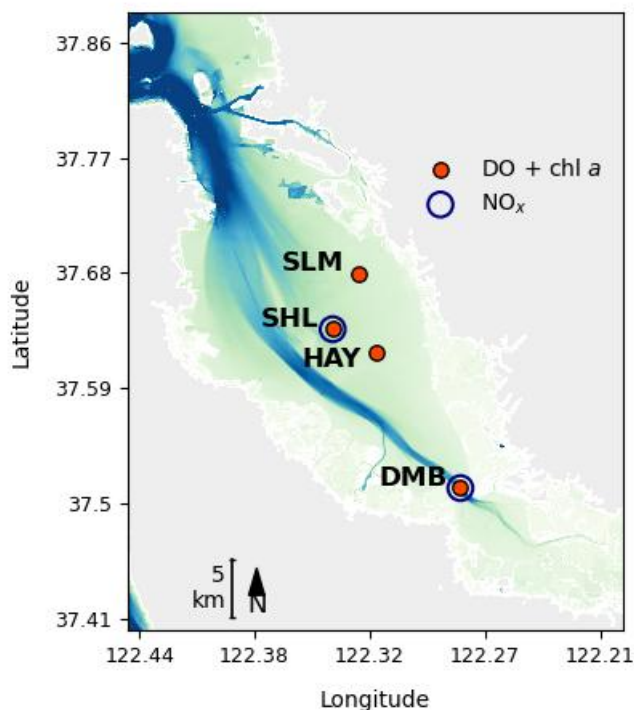
In densely populated coastal systems phytoplankton growth is fueled by excess nutrients, particularly DIN (Glibert et al., 2014). While not always the proximate cause of HABs, high DIN exacerbates HAB likelihood and severity (Bricker et al., 2008). DIN loading in urban watersheds is primarily attributed to agricultural runoff and industry (Carpenter et al., 1998). Major point sources include publicly owned treatment works (POTWs), which discharge DIN-enriched effluent following the purification of wastewater inputs (Holmes et al., 2019). Accordingly, reduced DIN loading is often a focus of POTW upgrades (Zhou et al., 2022). In aquatic systems, DIN and ecosystem metabolism are inextricably linked, as DIN fuels primary producer growth leading to enhanced production and respiration (Rabalais, 2002). Pairing estimates of HAB metabolism with estimates of DIN cycling helps elucidate the impact of DIN on HAB formation and dissipation.

San Francisco Bay (SFB) in California, USA is a coastal water body that drains a heavily urbanized and agricultural watershed. SFB receives substantial DIN loading from POTW discharge, with additional inputs from urban stormwater and agricultural runoff, resulting in high DIN on par with eutrophic systems (Cloern et al., 2020). SFB has historically avoided HABs and other algal overgrowth due to light limitation from high turbidity and strong turbulent mixing (Cloern et al., 2020). Typical phytoplankton dynamics have instead been largely defined by low baseline chlorophyll (chl) *a* levels ($<5 \mu\text{g L}^{-1}$) and regular spring blooms with chl *a* of $10\text{--}20 \mu\text{g L}^{-1}$ (Sutula et al., 2017). In August–September 2022 these paradigms broke down, and SFB experienced a massive bloom of the raphidophyte *Heterosigma akashiwo* (*Heterosigma*), representing the most severe HAB on record. The areal extent of the 2022 HAB was extensive, stretching more than 70 km from San Pablo Bay in the north to the Dumbarton Bridge in the south, with surface chl *a* concentrations as high as $530 \mu\text{g L}^{-1}$ (Nardelli et al., 2026). The 2022 HAB precipitated a substantial fish kill, both from direct impacts mid-event and from low DO following bloom collapse (Nardelli et al., 2026).

Understanding the underlying mechanisms and environmental impacts of the 2022 HAB is of paramount importance to SFB resource managers. In its role supporting nutrient-related decisions in the Bay, the SFB Nutrient Management Strategy (NMS) maintains a high frequency monitoring array of 8-14 water quality sondes. Four of these stations captured 15 min continuous DO and chl *a* data during the 2022 HAB, and two of them also recorded 15 min nitrate + nitrite (NO_x). The NMS, in partnership with the United States Geological Survey (USGS), also conducts regular boat-based high-speed water quality mapping cruises throughout SFB, including two cruises conducted during early and peak HAB conditions. The moored sensor data has high temporal resolution, allowing for NEM calculations, while the high-speed mapping data has high spatial resolution, allowing for basin-scale estimates of DIN utilization and phytoplankton growth. The goal of this study was to combine these datasets to estimate HAB NEM throughout its progression, as well as the total masses of chl *a* produced and DIN drawn down. Taken together, these results will help elucidate how high DIN fueled this historic event.

2. METHODS

2.1 STUDY SITE AND MOORED SENSOR ARRAY



*Figure 1 Map showing locations of EXO 2 (DO and chl *a*) and SUNA (NO_x) moorings in South San Francisco Bay (SB).*

The study site was the South Bay (SB) sub-embayment of SFB, which experienced some of the worst impacts from the 2022 HAB. Four SB sites from the NMS monitoring array were functional and captured data during the 2022 HAB (Fig. 1). These included three sites on the shallow eastern shoals: San Leandro Marina (SLM), Shoal (SHL), and Hayward (HAY), and one site in the deep channel: Dumbarton Bridge (DMB) (Fig. 1). At all four locations DO and chl *a* were recorded using YSI EXO2 multi-parameter sondes. At SHL and DMB, NO_x was recorded using Seabird SUNA V2 sensors. Raw NO_x values were corrected for temperature and salinity (Sakamoto et al., 2009) using data collected by the EXO, before being calibrated using discrete NO_x samples as described in Volaric et al. (2025). Both EXO2s and SUNAs continuously recorded data at 15 min intervals over the course of the event. NMS technicians regularly service these data

sondes every 3-5 weeks for data download and sensor cleaning / calibration, and all sonde data undergo rigorous QAQC (Volaric et al., 2025). Data are manually examined for signs of sensor fouling, defined as erratic jumps in values uncorrelated with tidal flows, with erroneous time periods removed.

2.2 ORGANIC CARBON (OC) FROM STOICHIOMETRIC RATIOS

Estimates of continuous organic carbon calculated from DO (OC_{DO}) and NO_x (OC_{NOx}) were defined as the cumulative sum of the difference between consecutive tidally filtered 15 min measurements, converted to molar units, and multiplied by the appropriate carbon (C) ratio (α). OC calculated from chl *a* (OC_{chl}) was defined as the tidally filtered chl *a* concentration multiplied by α_{chl} . As DO is reactive with the atmosphere, we added an additional correction for air-water transfer (F), described in the supplemental information (Section A2). The final equations for OC calculations for all three tidally filtered (filt) scalars were:

$$OC_{DO(t)} = \sum_{i=1}^t ([\Delta DO_{filt(t)} + F_t] * \alpha_{DO}) \quad (1)$$

$$OC_{chl} = chl_{filt} * \alpha_{chl} \quad (2)$$

$$OC_{NOx(t)} = \sum_{i=1}^t (-1 * \Delta NOx_{filt(t)} * \alpha_N) \quad (3)$$

where *t* represents the index of the appropriate time series coordinate.

Tidal filtering of the 15 min scalar data was performed using a 2nd order low-pass Butterworth filter with a cutoff frequency of 0.01 (Python Scipy package), equivalent to a cutoff period of 50 h. Error ranges of OC estimates were estimated by varying values of α . α_{DO} represents the combined molar quotient for photosynthesis and respiration by phytoplankton and heterotrophic bacteria, and ranged from a low of 0.67:1 to a high of 1.27:1 (Giorgio & Williams, 2005), with a mean of 1:1 (Glud, 2008). α_N is the molar ratio of C:N in phytoplankton biomass, and ranged from 5.5:1 to 10:1 (Burkhardt et al., 1999), with a mean of 6.6:1 (Redfield, 1934). α_{chl} is the mass ratio of C to chl *a* in phytoplankton biomass, and was calculated as the slope of the ordinary least squares (OLS) regression between particulate carbon (PC) and chl *a* discrete samples collected during high speed mapping cruises, which was 28:1 (Fig. S1). High and low values of α_{chl} were set to 50:1 and 20:1, respectively, based on past results from SFB (Cloern et al., 1995).

For each scalar and bloom phase, we calculated the mean change in OC concentration over time ($\frac{dOC}{dt}$), with the exception of $\frac{dOC_{NOx}}{dt}$, which we could only calculate for Phase 1 as NO_x was below detection limits during Phases 2 and 3. $\frac{dOC}{dt}$ for Phase 1 and Phase 3 were defined as the slope in OC between the 33rd and 66th percentiles in estimated OC for each scalar. $\frac{dOC}{dt}$ for Phase 2 was calculated from the 25th-75th percentile of time periods between the end of Phase 1 and the start of Phase 3.

$\frac{dOC}{dt}$ is attributed to two processes: HAB NEM and the dispersive flux (J_{disp}), with $\frac{dOC}{dt} = NEM + J_{disp}$. NEM is a biological process equivalent to the sum of algal gross primary production (GPP) and respiration (R), and represents the net *in situ* growth of *Heterosigma*, while J_{disp} is the physical transport of OC produced elsewhere. Open-water techniques for estimating aquatic metabolism often either directly measure J_{disp} by deploying multiple sensors in a given area (Nidzieko et al., 2014), or assume it is negligible following long-term averaging or other data manipulations (Beck et al., 2015; Caffrey, 2003). Unfortunately, given the short timeframe of the HAB (2-3 weeks) combined with our single-sensor measurements for each site, J_{disp} is not easily accounted for in our study, and we are unable to accurately separate the two signals from one another. Nevertheless, if we assume that the

original source of the HAB is outside our sensor footprints (i.e. $J_{disp} \geq 0$), as is currently believed (Senn et al *in prep*), $\frac{dOC}{dt}$ would represent upper-bound estimates of HAB NEM.

2.3 BASIN-SCALE ESTIMATES AND MASS BALANCES FROM HIGH-SPEED MAPPING DATA

As part of its SFB water quality monitoring efforts, the NMS, in partnership with the USGS, undertakes regular high-speed mapping cruises whereby a YSI EXO2 and Seabird SUNA V2 record water quality parameters just below the surface (~0.5 m) at 1 Hz using a flow-through system on a moving vessel (Richardson et al., 2025). Extra cruises were made to capture the impacts of the bloom, with two dates – 8/17/2022 and 8/25/2022 – constituting early and peak bloom conditions, respectively. Parameters recorded by high frequency sondes included DO, chl *a*, and NO_x. Discrete water quality samples were also collected during each cruise, including chl *a*, NO_x, ammonium (NH₄⁺), particulate carbon (PC), and phosphate (PO₄³⁻).

High-speed mapping data were used to calculate basin-scale estimates of total chl *a* produced and DIN utilized for all of SB, broadly defined as the Bay Bridge in the north to the Dumbarton Bridge in the south (latitude range = 37.5-37.8 °N). These data were spatially interpolated using the Krige function in the Python gstools package, with grid cell spacing of 0.01 degrees of latitude x 0.01 degrees of longitude (~1.1 km x 1.1 km). The mass of NO_x and chl *a* for each grid cell was estimated by multiplying their respective values by the grid cell area and mean water depth taken from bathymetry data. During the 8/25/2022 high-speed mapping survey we also measured a series of vertical chl *a* profiles. From these profiles we calculated the ratio of the depth averaged chl *a* to the chl *a* concentration at the sensor depth (0.5 m). This correction was applied to chl *a* from both 8/17/2022 and 8/25/2022 mapping surveys, but not to NO_x data, under the assumptions that phytoplankton had access to nitrogen across the entire vertical water column and that the chl *a* gradient was due to swimming behavior. Total mass of NO_x and chl *a* for all of SB was estimated by summing the totals from all grid cells. Due to the lower spatial resolution of NH₄⁺ measurements, the total mass of NH₄⁺ for each cruise was estimated as the mean NH₄⁺ concentration from discrete samples multiplied by the volume of SB.

The total masses of DIN utilized and chl *a* produced during the bloom ($\sum DIN_{HAB}$ and $\sum chla_{HAB}$) were estimated as:

$$\begin{aligned} \sum DIN_{HAB} &= (\sum NO_{xB} + \sum NH_{4B}^+) - (\sum NO_{xA} + \sum NH_{4A}^+) \\ \sum chla_{HAB} &= \sum chla_B - \sum chla_A \end{aligned} \quad (9,10)$$

where the subscripts A and B indicate early- and peak- bloom, respectively. $\sum DIN_{HAB}$ and $\sum chla_{HAB}$ were converted to units of OC ($\sum OC_{DIN}$ and $\sum OC_{chl}$, respectively) using the stoichiometric ratios described in Section 2.2.

3. RESULTS

3.1 PROGRESSION OF HAB EVENT

The HAB followed a distinct progression characterized by three phases evident at all sites in the DO, chl *a*, and NO_x time series data. The three phases are depicted for SHL in Fig. 2ABC, and are defined as follows:

- Phase 1 (Rapid growth): Phase 1 of the bloom was defined by rapid growth of phytoplankton. DO and chl *a* concentrations sharply increased, with DO becoming supersaturated, while NO_x was fully depleted. The length of this phase ranged from 4-12 days based on sensor location.
- Phase 2 (Slowed growth): Phase 2 began once DIN was depleted. Supersaturated DO levels gradually decreased, primarily due to exchange with the atmosphere. Chl *a* concentration continued to increase, but at a slower rate than during Phase 1. The length of Phase 2 ranged from 6-8 days based on sensor location. Please note that NO_x at SHL was exhausted ~1-2 days before onset of Phase 2 in DO and chl *a* data. This time lag is attributed to uptake of NH₄⁺, which was only measured with discrete water samples.
- Phase 3 (Bloom collapse): Phase 3 represents the collapse of the HAB, defined by the mass death of phytoplankton. Chl *a* and DO rapidly decreased, leading to water column hypoxia and anoxia. The length of Phase 3 was approximately 2 days.

There was a temporal lag in the onset of Phase 1 across the four stations as the bloom progressed across SB (Fig. 3). SHL was the first station impacted, with Phase 1 beginning on Aug. 12, 2022, followed by SLM (Aug. 17), HAY (Aug. 18), and DMB (Aug. 20) (Fig. 3 A-D). Interestingly, the progression of the HAB did not proceed along a clear longitudinal gradient, as SHL lies between SLM and HAY along the N-S axis (Fig. 1A). Despite the lag in onset, the bloom collapsed nearly simultaneously at all four locations on Aug. 29-31.

All sites demonstrated large ranges in DO and chl *a* concentration in accordance with the three phases (Fig. 2DEF). Maximum DO recorded during peak bloom conditions at the end of Phase 1 ranged from 188-230 % sat (13.6 - 16.4 mg L⁻¹) across the four sites, while minimum DO recorded at the end of Phase 3 following bloom collapse ranged from 1.4-36 % sat (0.1-2.6 mg L⁻¹). Likewise, maximum chl *a* concentration measured at the end of Phase 2 ranged from 111- 179 µg L⁻¹ at the four sites. Maximum pre-bloom NO_x values recorded by the SUNAs were 24 and 32 µM at SHL and DMB, respectively, and were fully depleted at both sites following Phase 1. The above ranges are based on unfiltered 15 min data.

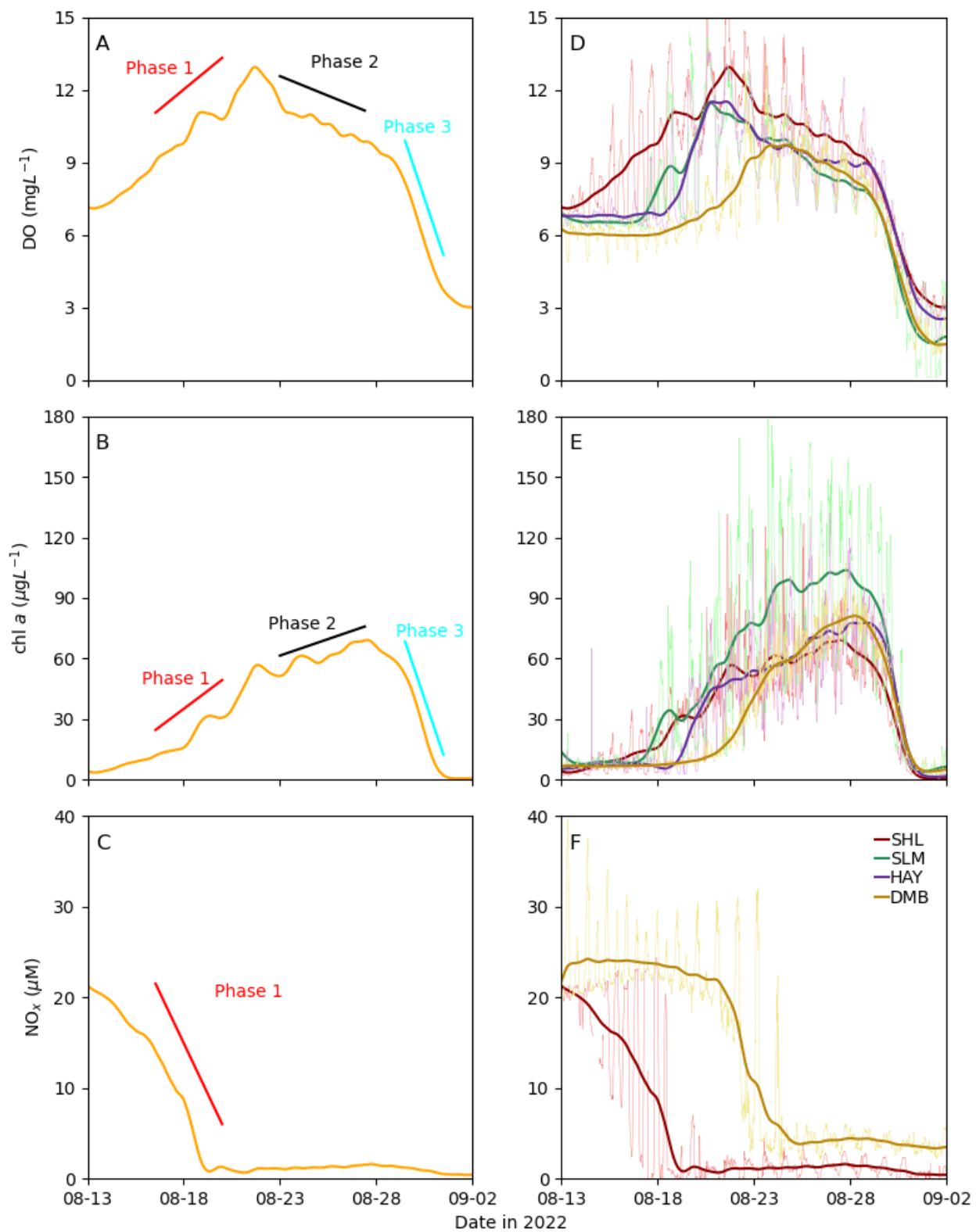


Figure 2 Progression of the bloom at SHL depicting the three phases in the tidally filtered DO (A), chl a (B), and NO_x (C) time series. These phases were evident at all four sites in the DO (D), chl a (E), and NO_x (F) datasets. In panels D-F the light lines represent 15 min data, and the dark lines are tidally filtered.

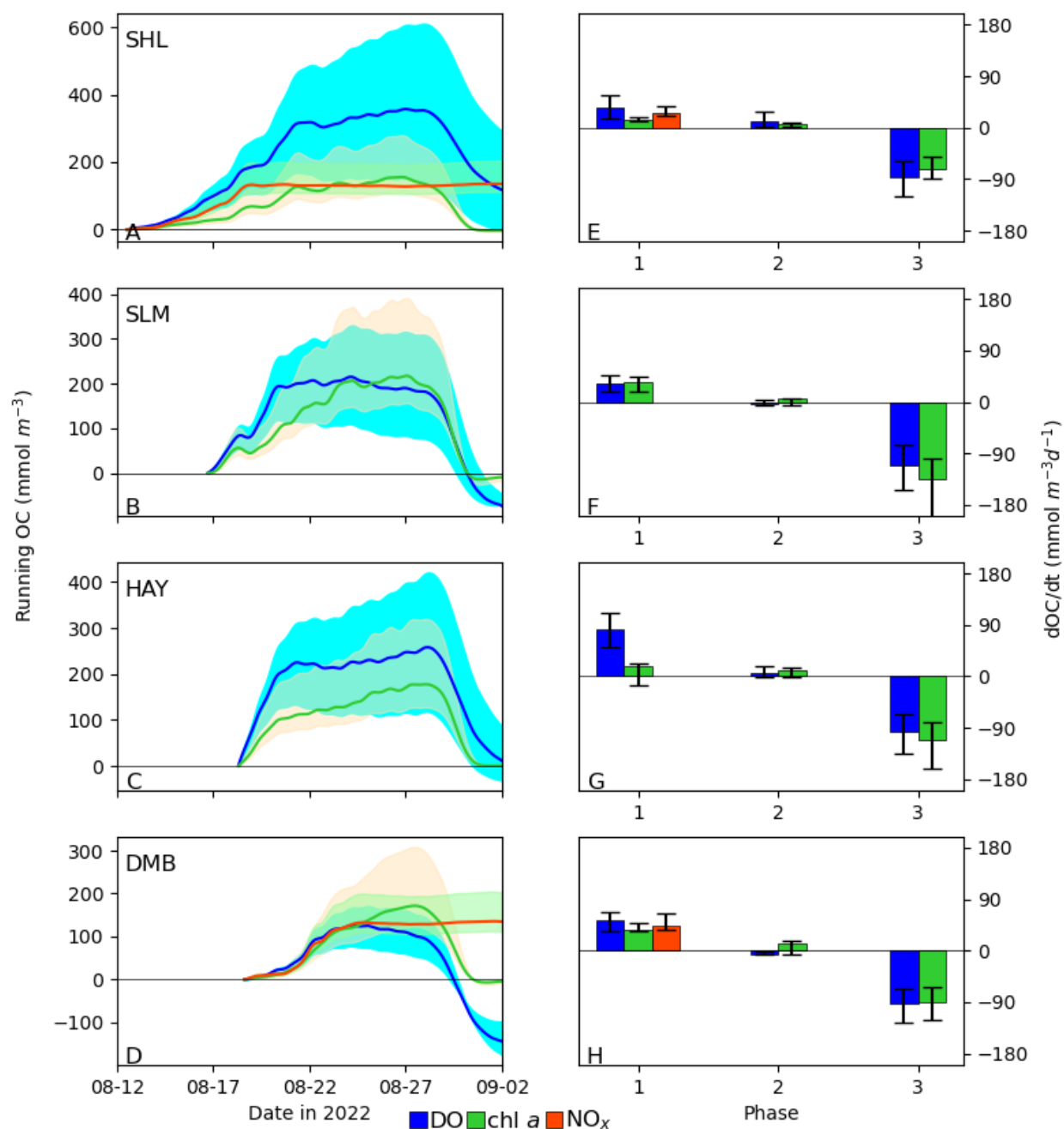


Figure 3 Volumetric estimates of water column organic carbon (OC) at the 4 moored sensor locations during the HAB (A-D). Solid lines are OC estimates calculated using the mean α for each scalar, while shaded areas show range between high and low estimates. The slope of OC over time was calculated for each of the three bloom phases (E-H), and represents the sum of in situ phytoplankton NEM and the dispersive flux.

3.2 OC AND NET ECOSYSTEM METABOLISM

Estimates of continuous OC are summarized in Fig. 3. Phase 1 $\frac{dOC_{DO}}{dt}$ ranged from 34 - 82 mmol m⁻³ d⁻¹ across the 4 sites, showing strong agreement with $\frac{dOC_{NOx}}{dt}$ (24 - 43 mmol m⁻³ d⁻¹), however, $\frac{dOC_{chl}}{dt}$ tended to be less (13 - 37 mmol m⁻³ d⁻¹). During Phase 2, $\frac{dOC_{DO}}{dt}$ ranged from weakly positive to weakly

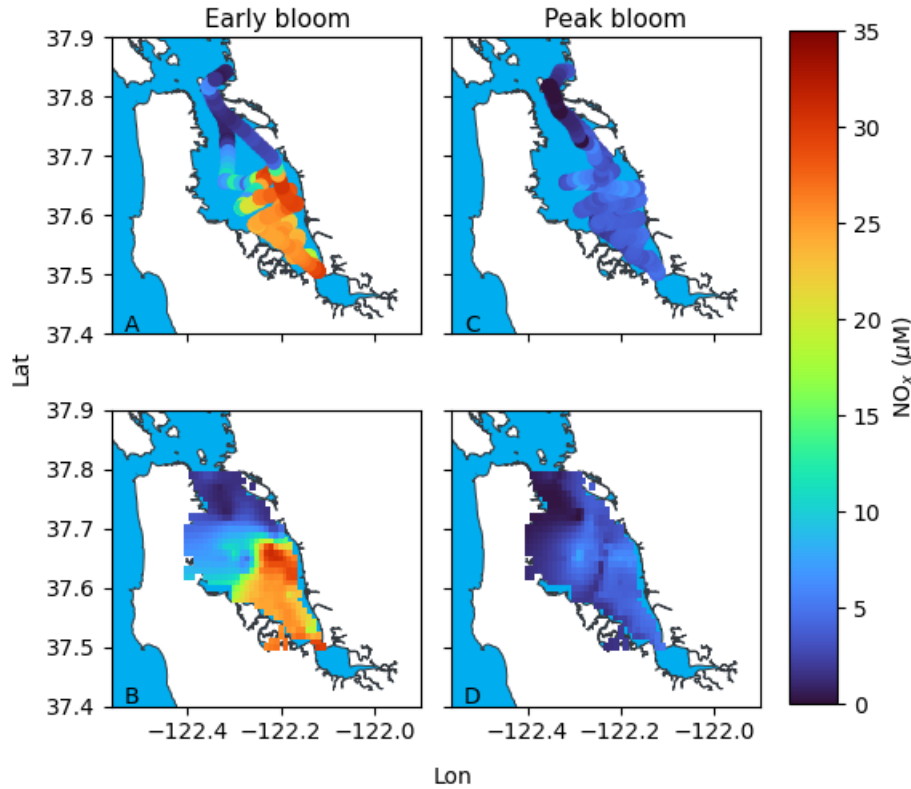


Figure 4 High speed mapping (A,B) and spatially interpolated (B,D) NO_x measurements during early bloom and peak bloom conditions. The early bloom mapping trip occurred on 8/17/2022, after the bloom had begun in the in the upper SB near Alameda Island. The date of the peak bloom mapping survey was 8/25/2022.

remineralization of phytoplankton OC.

For all scalars $\frac{dOC}{dt}$ is composed of NEM and J_{disp} . J_{disp} is driven by spatial gradients in scalar concentration, which are correlated to tidal fluctuations in the 15 min data (Fig. 2DEF). These fluctuations were greatest during Phase 1 and Phase 2, and much smaller in Phase 3 during bloom collapse. Therefore, $\frac{dOC}{dt}$ during Phase 3 likely approximates true values of phytoplankton NEM during bloom collapse. For all three phases, $\frac{dOC}{dt}$ represents upper bound estimates of phytoplankton NEM.

negative depending on site (-5 - 12 mmol m⁻³ d⁻¹), while $\frac{dOC_{chl}}{dt}$ was weakly positive at all sites (5-13 mmol m⁻³ d⁻¹). $\frac{dOC_{DO}}{dt}$ was strongly negative during Phase 3 (-87 - -110 mmol m⁻³ d⁻¹), showing strong agreement with $\frac{dOC_{chl}}{dt}$ (-72 - -136 mmol m⁻³ d⁻¹). Strongly positive $\frac{dOC}{dt}$ measured from all scalars at all sites during Phase 1 indicates rapid bloom growth, $\frac{dOC}{dt}$ close to 0 in Phase 2 is consistent with slow growth and/or stasis, and strongly negative $\frac{dOC}{dt}$ during Phase 3 consistent with bloom collapse and rapid

3.3 BASIN-SCALE PHYTOPLANKTON GROWTH AND DIN UTILIZATION

Basin-wide NO_x concentration fell from 20-30 $\mu\text{M N}$ during early bloom conditions to near zero during the peak bloom (Fig. 4). $\text{Chl } a$ concentration increased from 5-10 $\mu\text{g L}^{-1}$ to 30 - 220 $\mu\text{g L}^{-1}$ (Fig. 5). These concentrations include a correction for the ratio of the mean surface to depth-integrated concentration, which across all vertical sonde casts was equal to 0.74 (Fig. S2). Mean NH_4^+ from discrete water samples fell from 2.1 to 0.4 $\mu\text{M N}$ (Table 1).

The total masses of NO_x in SB estimated from spatial interpolation of mapping data were 400 and 95 Mg N during early and peak bloom conditions, respectively (Fig. 6). Including NH_4^+ , the total

Table 1 Summary of discrete sample results for various constituents during the two high-speed mapping surveys. Values are mean $\pm$ SD (n).

Parameter	Mapping Date	
	8/17/2022	8/25/2022
NO_x ($\mu\text{M N}$)	13.6 ± 1.5 (34)	0.17 ± 0.03 (64)
NH_4 ($\mu\text{M N}$)	2.1 ± 0.2 (34)	0.4 ± 0.02 (64)
TDN ($\mu\text{M N}$)	27.8 ± 2.2 (18)	27.0 ± 2.0 (18)
PO_4^{3-} ($\mu\text{M P}$)	5.0 ± 0.4 (34)	3.3 ± 0.2 (64)
$\text{chl } a$ ($\mu\text{g L}^{-1}$)	24.2 ± 4.0 (18)	141 ± 29 (18)

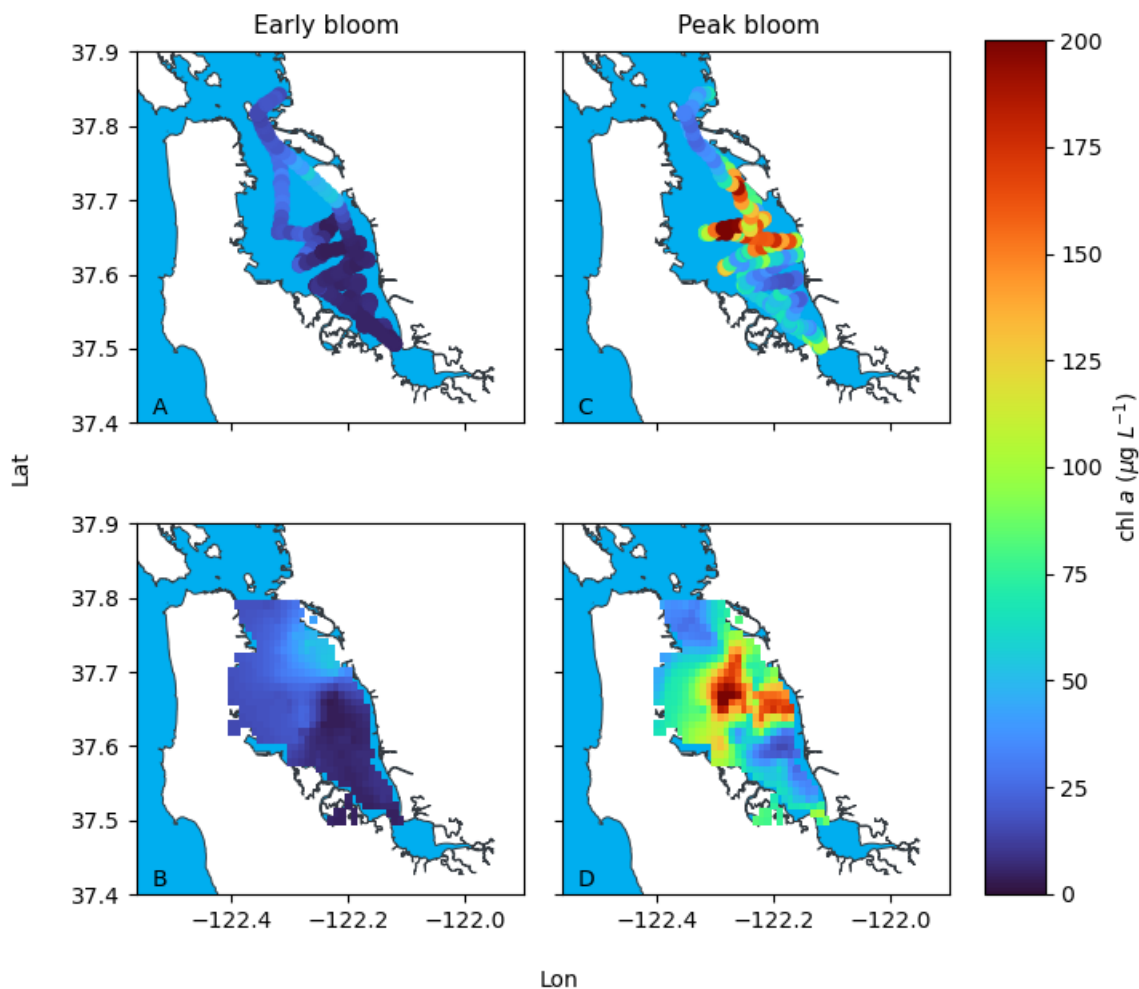


Figure 5 High speed mapping (A,B) and spatially interpolated (B,D) $\text{chl } a$ measurements during early bloom and peak bloom conditions. The early bloom mapping trip occurred on 8/17/2022, after the bloom had begun in the in the upper parts of SB near Alameda Island. The date of the peak bloom mapping survey was 8/25/2022.

masses of DIN were 500 and 110 Mg, respectively, indicating a drawdown of 390 Mg during this time period (Fig. 6). Total masses of chl *a* during pre and peak bloom conditions were 60 and 230 Mg, respectively, indicating a gain of 170 Mg (Fig. 6). $\sum OC_{DIN}$ was considerably less than $\sum OC_{chl}$, at 2,150 Mg C (1,800 – 3,250 Mg C) and 4,700 Mg C (3,350 – 8,400 Mg C), respectively, with the value ranges defined by the range of stoichiometric ratios described in Section 2.4. This excess OC suggested by chl *a* biomass above what could be supplied by the initial stock of DIN is attributed primarily to ongoing DIN loading from POTWs during the 8 days between high speed mapping cruises (see Discussion below).

4. DISCUSSION

4.1 IMPACTS OF 2022 HAB ON SFB

Our results indicate that the 2022 HAB utilized nearly all of the substantial pre-bloom standing stock of DIN within SB, with both mooring and high-speed mapping data showing a drawdown of NO_x from a pre-bloom concentration of $\sim 30 \mu M$ to near zero over the course of the event (Fig. 2, Fig. 4, Table 1). Of the three bloom phases, the first two (rapid and slowed growth) are tied to DIN availability. When Phase 1 began, DIN was abundant in the water column, meaning N was non-limiting to *Heterosigma* and it grew rapidly. There was a slight lag between NO_x depletion and the onset of Phase 2 (Fig. 2), likely due to uptake of NH_4^+ (Table 1, Fig. 6A). The inflection points to the flatter slopes and slower growth that indicate the onset of Phase 2 coincided with low, likely limiting levels of DIN.

The slowed growth that defined Phase 2 was likely supported by ongoing DIN loading from POTWs that occurred throughout the 2022 HAB. Phase 2 $\frac{dOC_{DO}}{dt}$ ranged from $-5 - 12 \text{ mmol m}^{-3} \text{ d}^{-1}$ between sites, while $\frac{dOC_{chl}}{dt}$ was somewhat greater, ranging from 5 to 13 mmol m^{-3} (Fig. 3). N loading from POTWs to SB is $\sim 30 \text{ Mg N d}^{-1}$, equivalent to $0.7 \mu M \text{ d}^{-1}$ when expressed over the total volume of SB (2.95 km^3). Applying our α_N of 6.6:1, and assuming that N is efficiently recycled within the HAB such that all incoming DIN from POTWs fueled Phase 2 growth, the estimated NEM for Phase 2 from POTW discharge would be $4.8 \text{ mmol m}^{-3} \text{ d}^{-1}$, solidly in the range of

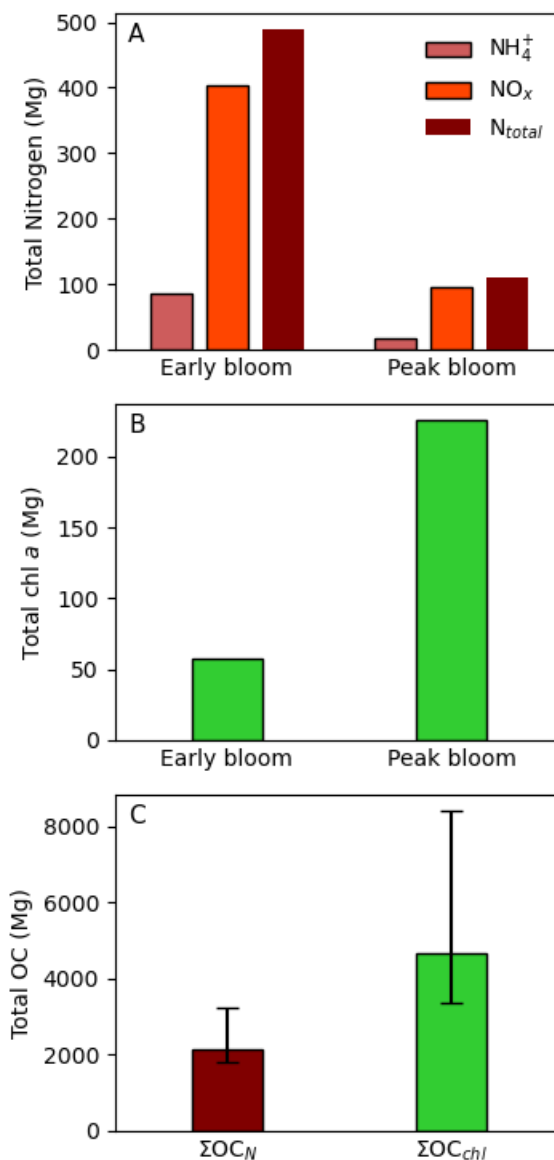


Figure 6 Basin-wide estimates of total mass of (A) DIN, (B) chl *a*, and (C) estimated organic carbon (OC) from each of these scalars. Our estimate of total OC from chl *a* is substantially higher than that from DIN drawdown, likely due to ongoing DIN loading from POTWs.

$\frac{dOC_{DO}}{dt}$ and at the lower end $\frac{dOC_{chl}}{dt}$. Ongoing nutrient loading sustaining the HAB is supported by a difference of 2,500 Mg between $\sum OC_{DIN}$ and $\sum OC_{chl}$ (Fig. 6). This quantity of OC is equivalent to 450 Mg N, reasonably close to the ~240 Mg N that are estimated to have been discharged by POTWs over the course of the HAB. It should be noted that DIN in the Lower South Bay south of the Dumbarton Bridge (Fig. 1) was not captured by our high-speed mapping cruises (Fig. 3), yet would have been available to *Heterosigma* cells during the HAB, further explaining the gap between $\sum OC_{DIN}$ and $\sum OC_{chl}$.

DIN concentration – and by extension nutrient limitation – does not explain the collapse of the 2022 HAB (Phase 3). Despite DIN being depleted nearly a week prior at the SHL vs. DMB moorings, the bloom collapsed simultaneously at both sites, along with SLM and HAY. As ongoing DIN loading to SB likely sustained the HAB during Phase 2, it presumably would have continued to do so outside of an additional external pressure. The crash also cannot be attributed to phosphorus (P) depletion, as the initial stock of PO_4^{3-} only decreased by ~35% during the HAB (Table 1), suggesting N limitation throughout. The ultimate cause of the HAB collapse is unclear, but a key hypothesis that we are currently investigating is that it was instigated by a top-down pressure, such as the growth of predatory zooplankton or a marine virus. Marine viruses in particular have been found to precipitate phytoplankton bloom collapses at times of low N but non-limiting P (Bratbak et al., 1993), including *Heterosigma* blooms (Lawrence & Suttle, 2004), and would explain concurrent signals between $\frac{dOC_{DO}}{dt}$ and $\frac{dOC_{chl}}{dt}$ for Phase 3. DO depletion was coincident with the collapse of chl *a*, suggesting that the death of phytoplankton produced a massive pulse of highly labile OC that was rapidly remineralized by heterotrophic bacteria. Such highly labile OC is consistent with viral lysis and the bursting of algal cells, but not with the simple death and settling of *Heterosigma* out of the water column to the sediment surface, nor with the consumption of *Heterosigma* by a higher trophic level (Gobler et al., 1997).

One key management question related to the HAB is the impact of local growth vs. transport on HAB progression, i.e., did a single source location seed *Heterosigma* to other regions of SFB via hydrologic transport, or did conditions within the Bay allow for *Heterosigma* to spontaneously grow across a wide area? The 2022 HAB event is believed to have originated near Alameda Island ~10 km north of the SLM mooring, before spreading to other regions of SFB including SB (Senn et al, *in prep*). Although not definitive, our results suggest that the HAB may have progressed by initial seeding from this source location followed by continued *in situ* growth at new locations. Large swings in the 15 min chl *a*, DO, and NO_x data during Phases 1 and 2 (Fig. 2 DEF) suggest large J_{disp} and that physical transport played a substantial role during these periods of bloom progression, while the comparatively smaller swings during Phase 3 are consistent with small J_{disp} and *in situ* bloom collapse across all regions of SFB. In other words, during Phases 1 and 2 the bloom likely expanded due to a combination of hydrologic transport and *in situ* growth, but during Phase 3 the bloom collapsed in all places at approximately the same time.

4.2 HAB METABOLISM FROM HIGH FREQUENCY DATA

In our study were unable to estimate J_{disp} , and as a result values of $\frac{dOC}{dt}$ represent high-end – rather than true – estimates of SB NEM. However, results from our high-speed mapping data suggest

that J_{disp} may be negligible over large spatiotemporal scales. We can estimate NEM from the high-speed mapping results (NEM_{map}) using the difference in $\sum OC_{chl}$, the time between the mapping trips (dt), and the volume of SB (V), as $NEM_{map} = d\sum OC_{chl}/V * dt$. Doing so results in an NEM_{map} of $17 \text{ mmol m}^{-3} \text{ d}^{-1}$, a value that is fully independent of our moored sensor results. $\frac{dOC_{chl}}{dt}$ calculated over same time period as the mapping cruises (8/17/2022 – 8/22/2022) ranges from $14 - 26 \text{ mmol m}^{-3} \text{ d}^{-1}$ between the 4 stations, showing strong agreement with NEM_{map} and suggestive of the fact that taken as a whole, our values of $\frac{dOC}{dt}$ broadly represent HAB NEM. Nevertheless, J_{disp} still likely explains much of difference in $\frac{dOC}{dt}$ values between sites, and was likely most consequential during Phase 1 when the scalar spatial gradients were largest.

This study represents one of the first efforts to quantify the metabolism of a major HAB at the ecosystem scale. NEM estimates approximated from $\frac{dOC}{dt}$ are similar in principle to diel open-water metabolic estimates based on DO (Staehr et al., 2010), in that both are based on time varying concentrations of ecosystem scalars. Our methodology has the advantage of utilizing three independent NEM estimates, allowing for inter-comparison and/or estimates of HAB metabolism when DO data are absent, but chl a or NO_x data are available. Diel estimates in dynamic environments such as estuaries also often require longer-term averaging or complex curve fitting to account for advection of DO (Beck et al., 2015), making them unsuitable for transient events such as HABs.

Applying the correct stoichiometric ratios is crucial when converting environmental scalars to OC. DO-based NEM estimates typically assume a 1-to-1 molar ratio for α_{DO} (Berg et al., 2022), although ranges as wide as 0.67-1.24 have been observed for biologic material (Giorgio & Williams, 2005). α_N for phytoplankton is often close to Redfield ratio of 6.6:1 (Redfield 1934), although they too can vary as much as 5:1 – 10:1 based on species and nutrient availability (Burkhardt et al., 1999). Values of α_{chl} tend to be species specific, with typical ranges of 20:1 – 100:1 (Cloern et al., 1995). We calculated a α_{chl} of 28:1 based on discrete water quality samples (Fig. S1), which is within the range previously observed for SFB (Cloern et al., 1995; Hoshovsky et al., 2025). Unlike α_{DO} or α_N , α_{chl} can change substantially as phytoplankton production increases, with α_{chl} likely to decrease as phytoplankton produce more chlorophyll per algal cell to combat self-shading (Falkowski & Owens, 1980). A negative correlation between α_{chl} and phytoplankton production has in fact been observed in SFB and other systems, albeit over monthly to annual timescales (Hoshovsky et al., 2025; Jakobsen & Markager, 2016). For the 2022 HAB, a decreasing α_{chl} would explain the disconnect between $\frac{dOC_{chl}}{dt}$ with $\frac{dOC_{DO}}{dt}$ and $\frac{dOC_N}{dt}$ during Phase 1. Over the course of our analysis we explored several methods to incorporate a variable α_{chl} , with some success, and hope to add a variable α_{chl} to future iterations of this work.

5 Conclusions

Our study provides a novel exploration of the interplay between OC and DIN during a HAB at the ecosystem scale. Although the proximate cause of the HAB remains a topic of much debate (Senn et al, *in prep*), our results show that a high standing stock of DIN fueled the immense scale of the event, which included bay-wide DIN drawdown, high chl a , and supersaturation of DO followed by widespread

anoxia/hypoxia. Prior to 2022, SFB was believed to be resistant to HABs due to its high turbidity and strong turbulent mixing. As shown by the HAB, it is clear that these protections can no longer be counted on by resource managers. By demonstrating the complete utilization of SB DIN by phytoplankton, our results support the need for upcoming permit-required POTW load reductions to SFB, as lower nutrient levels will decrease the maximum severity of future HABs. The methodologies developed here can aid the monitoring and analysis of future HABs, both in SFB and beyond.

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APPENDIX

A1: FIGURES

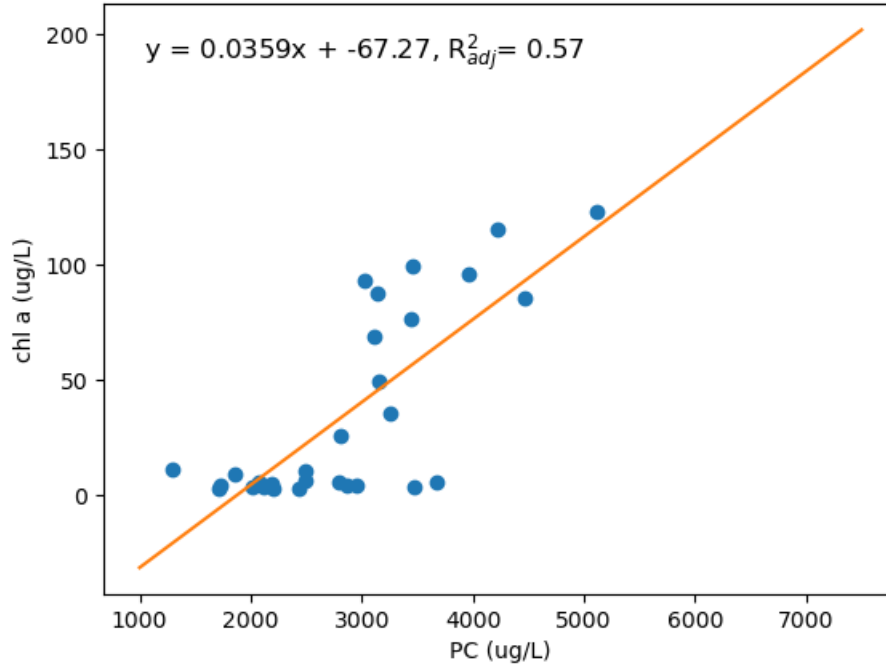


Figure S1: Best fit of discrete particulate carbon (PC) vs discrete chl a. The slope of the best fit line (0.036) represents α_{chl} , which was used to convert chl a concentration to units of OC. Discrete samples were collected during high-speed mapping trips during the period of the 2022 HAB. To prevent bias from large chl a out of range of sensor values, best fit only includes chl a < 150 $\mu\text{g L}^{-1}$.

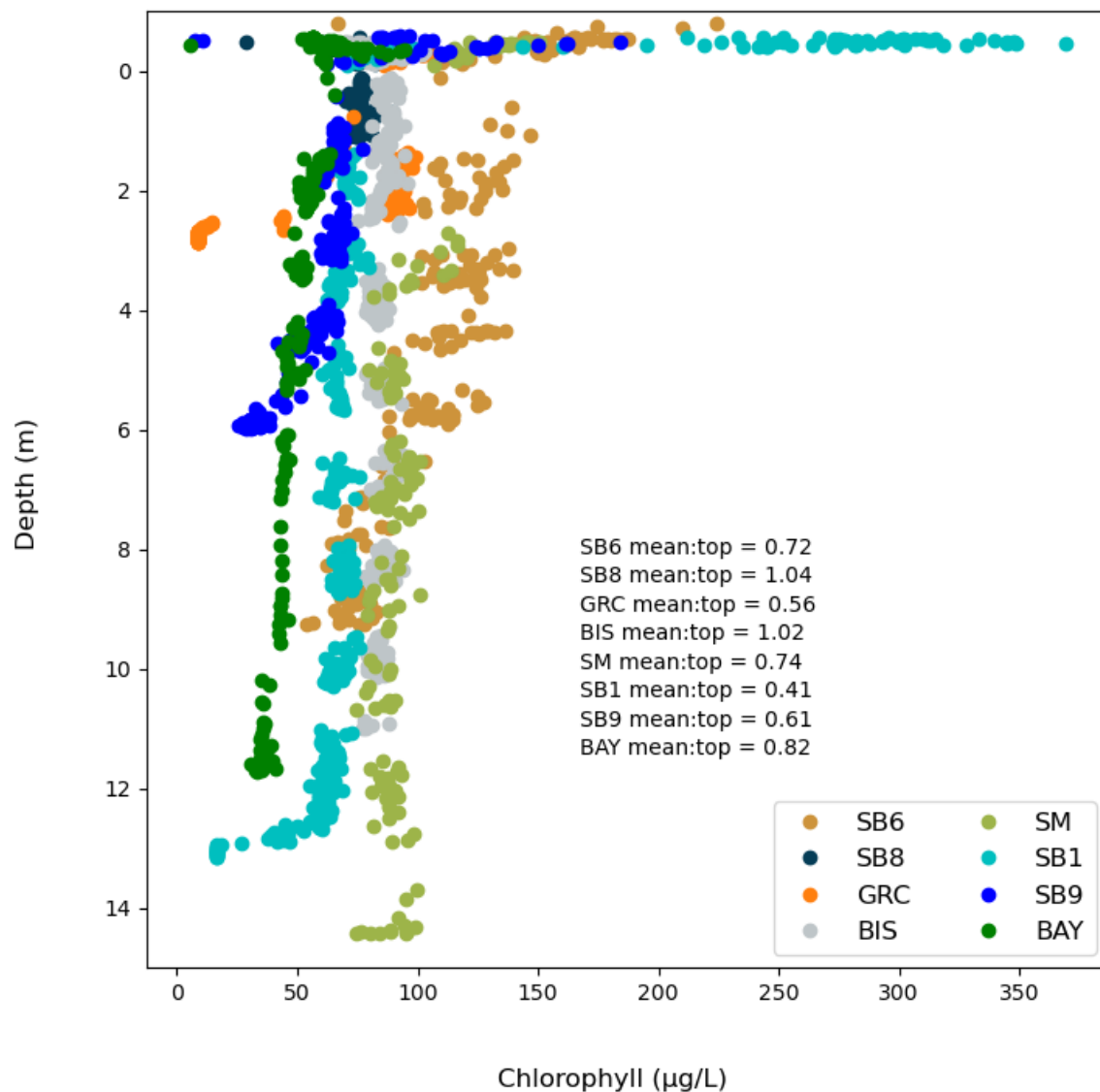


Figure S2 Vertical profiles of chl a measured at 8 locations during 8/25/2022 mapping survey. Each color refers to a different location in SB. The mean ratio between surface values to transect mean was 0.74. This correction was used to correct high speed mapping chl a data collected at the surface when estimating basin-wide chl a biomass for all of SB.

A2: AIR-GAS TRANSFER (F)

Unlike chl a and NO_x , DO is a reactive tracer that mixes with the atmosphere. Estimates of OC_{DO} requires an estimate of atmosphere transfer of DO (F). F was calculated from the piston velocity for air-water gas transfer (k) and DO saturation as described by Staehr et al. (2010):

$$F = k \times (DO_{\text{meas}} - DO_{\text{sat}}) \quad (\text{A1})$$

where DO_{meas} is the measured DO value and DO_{sat} is the saturation concentration. The k value was calculated as (Jähne et al., 1987; Staehr et al., 2010) :

$$k = k_{600} \times \left(\frac{Sc}{600} \right)^{-0.5} \quad (\text{A2})$$

where k_{600} is the piston velocity normalized to a Schmidt number (Sc) of 600, and is equal to (Cole & Caraco, 1998; Staehr et al., 2010):

$$k_{600} [m\ h^{-1}] = \frac{2.07 + 0.215 U_{10}^{1.7} [m\ s^{-1}]}{100} \quad (\text{A3})$$

In this equation U_{10} the wind speed measured at 10 m above the surface, taken from California Irrigation Management Information System (CIMIS) website (<https://cimis.water.ca.gov/WSNReportCriteria.aspx>). Sc was calculated based on water temperature (T, Celsius) (Staehr et al., 2010; Wanninkhof, 1992):

$$Sc = 0.0476 T^3 + 3.7818 T^2 - 120.1 T + 1800.6 \quad (\text{A4})$$