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Biogenic silica cycling during summer phytoplankton blooms in the North Pacific subtropical gyre

Jeffrey W. Krause [a,*], Mark A. Brzezinski [a,b], Tracy A. Villareal [c], Cara Wilson [d]

[a] Marine Science Institute, University of California, Santa Barbara, CA, USA
[b] Department of Ecology Evolution and Marine Biology, University of California, Santa Barbara, CA, USA
[c] Marine Science Institute and the Department of Marine Science, The University of Texas, Austin, Port Aransas, TX, USA
[d] NOAA/NMFS/SWFSC Environmental Research Division, Pacific Grove, CA, USA

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ABSTRACT

Biogenic silica ($bSiO_2$) cycling, diatom abundance and floristics were examined within summer-period diatom blooms in the North Pacific Subtropical Gyre (NPSG) in 2008 and 2009. *Hemiaulus hauckii* was the most abundant diatom observed in an expansive (100,000 km^2) bloom near the subtropical front in the northeastern NPSG in 2008 and the small pennate diatom *Mastogloia woodiana* dominated a smaller (30,000 km^2) bloom sampled in 2009 in the gyre interior. In both blooms, the $bSiO_2$ stock and production rates were up to an order of magnitude higher relative to non-bloom areas. Remnants of a $bSiO_2$ export event was sampled in the *H. hauckii* bloom area where the export rate at 300 m exceeded that at 150 m, and was among the highest values recorded in the NPSG. The *M. woodiana* bloom was very active with specific $bSiO_2$ production rates of 0.50–0.75 d^{-1} and net $bSiO_2$ production rates were among the highest observed in any subtropical-gyre diatom bloom to date. Net silica production rates in the euphotic zone were strongly positive within blooms and near zero outside of blooms, consistent with an important role for blooms in $bSiO_2$ export. The difference in the areal extent of the *H. hauckii* and *M. woodiana* blooms was consistent with remote-sensing observations that blooms in the northeastern portion of the NPSG, near the subtropical front, are typically more extensive than those in the gyre interior near Hawaii Ocean Time-series station ALOHA. Initial estimates suggest that blooms in the northeast region produced 3–25 times more $bSiO_2$ in 2008 and 2009, respectively, than did blooms in the gyre interior; and due to the large areal extent these blooms, their area-integrated production of $bSiO_2$ is similar to intense diatom blooms coastal upwelling systems (e.g. Monterey Bay, Santa Barbara Channel) despite significantly lower production rates and standing stock.

1. Introduction

Compared to blooms in other subtropical gyres, phytoplankton blooms in the North Pacific subtropical gyre (NPSG) are different in their timing and in the hydrographic conditions under which they occur. Winter convective mixing in the NPSG is weak and regular spring blooms do not ensue; instead, phytoplankton blooms occur during summer when the upper-water column stratification is at its annual maximum and macronutrient concentrations are at their annual minimum (Wilson, 2003; Dore et al., 2008; Wilson et al., 2008). This situation sharply contrasts with that in the North Atlantic Subtropical Gyre (NASG) where strong winter convection typically erodes the pycnocline and entrains nutrients into the euphotic zone, thereby stimulating a regular spring bloom after water-column restratification (Sverdrup, 1953). Summer blooms in the NPSG interior show enhanced abundance of diazotrophs (e.g. *Trichodesmium*) and diatoms (Dore et al., 2008; Fong et al., 2008; Villareal et al., 2011, 2012); however, *Trichodesmium* is rarely observed in the northeastern NPSG near the subtropical front (Venrick, 1997; Dore et al., 2008) where satellite ocean color observations reveal blooms that are generally more expansive and that longer-lived than those in the gyre interior near the Hawaii Ocean Time-series (HOT) station ALOHA (Wilson, 2003; Wilson et al., 2008). At least some of the blooms occurring in the northeastern gyre are dominated by diatoms (Brzezinski et al., 1998; Villareal et al., 2011).

Why diatom blooms in the NPSG occur during the highly oligotrophic conditions of summer remains enigmatic. Some blooms contain diatom-diazotrophic associations (DDAs, e.g. the diatom genera *Hemiaulus* or *Rhizosolenia* and the nitrogen-fixing symbiont, *Richelia*; Villareal et al., 2011), suggesting that the biological input of fixed N may play a role in bloom initiation and development. Recently, it was also suggested that summer blooms in the northeastern NPSG can occur in response to

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* Corresponding author. Tel.: +1 805 893 7061; fax: +1 805 893 8062.
E-mail address: jeffrey.krause@lifesci.ucsb.edu (J.W. Krause).

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increased vertical mixing due to internal wave breakdown at the 30°N "critical latitude" (Wilson, 2011). A diatom bloom also requires adequate silicic acid; relative to the nanomolar levels of inorganic N and P in the surface waters of the NSPG, the silicic acid requirement is easily met as surface-water concentrations are typically 0.5–1.5 μM. There is also evidence that the diatom taxa which dominate summer blooms have very efficient Si uptake kinetics, such that ambient silicic acid concentrations of ~1 μM would support high growth rates (Brzezinski et al., 1998; Krause et al., 2012).

While there currently is no consensus on the factor(s) initiating summer diatom blooms in the NPSG, there is clear evidence as to their importance in annual biogeochemical budgets. This is somewhat counter intuitive as diatom biomass during non-bloom periods at station ALOHA, as measured by biogenic silica ($bSiO_2$) concentration, is the lowest thus far observed in the global ocean (Brzezinski et al., 2011). However, at the HOT station ALOHA the contribution of diatoms to new production exceeds both their contribution to autotrophic biomass and their estimated contribution to primary production (Brzezinski et al., 2011), implying a disproportionately important role for diatoms in carbon export. This is especially true for summer blooms which have been estimated to account for 18% of annual new production at station ALOHA (Dore et al., 2008) and recent estimates suggest that summer blooms account for 29% of the annual production of $bSiO_2$ at ALOHA (Brzezinski et al., 2011). Blooms in the northeastern gyre near the subtropical front are typically longer-lived than those at or near ALOHA (Wilson et al., 2008), but their role in annual biogeochemical budgets is less clear. There is also evidence for a significant role for diatoms in the export of carbon to the ocean interior at ALOHA where observations from both shallow (150 m) and deep (≥ 2800 m) sediment traps show an annual summer maximum in carbon export associated with increased diatom and $bSiO_2$ export (Scharek et al., 1999a, 1999b; Karl et al., 2012). To further evaluate the contribution of summer diatom blooms to silica production and organic matter cycling in the NPSG, we examined rates of gross and net silica production, diatom abundance and taxonomic composition within summer phytoplankton blooms in the NPSG.

2. Methods

2.1. Study area and sampling

The Pacific Open-Ocean Bloom (PB) cruises were conducted aboard the R/V *Kilo Moana* from 4–19 July 2008 (PB08) and from 29 July–12 August 2009 (PB09). Using daily composite images from the Moderate Resolution Imaging Spectroradiometer (MODIS, http://modis.gsfc.nasa.gov), bloom regions were identified as areas with chlorophyll a (Chl *a*) concentrations $\geq 0.12\ \mu g\ L^{-1}$. As the feature sampled in 2008 was relatively weak, visualizing the full extent of the bloom area required the [Chl *a*] threshold value to be slightly lower than the $0.15\ \mu g\ L^{-1}$ value used previously (Wilson et al., 2008); for consistency we use the same [Chl *a*] threshold for both PB cruises. Three regions with bloom-level [Chl *a*] were sampled, one in 2008 and two in 2009. Within each bloom region, stations were classified as representing a diatom bloom condition by meeting two criteria: (1) the $>10\ \mu m$ size-fraction [Chl *a*] was >30% of the total [Chl *a*] collected on a $>0.4\ \mu m$ filter. This threshold value represents a three-fold increase in $>10\ \mu m$ [Chl *a*] fraction over that present under non-bloom conditions in the gyre during summer (Villareal et al., 2011), and (2) diatom numerical abundance exceeded 1000 cells L^{-1}, consistent with threshold bloom abundances previously applied in this region (e.g. Brzezinski et al., 1998; Villareal et al., 2011).

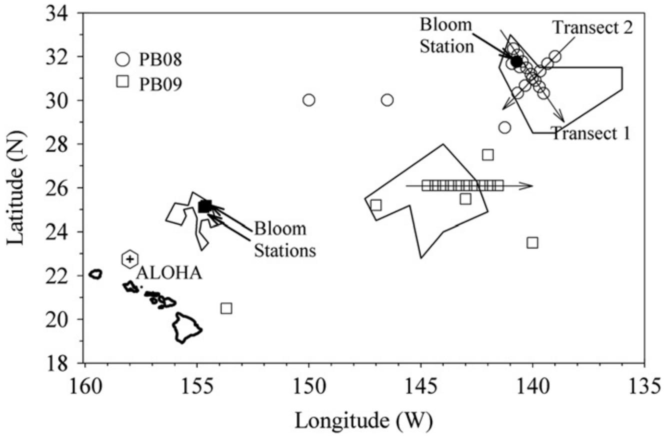

Fig. 1. Station locations during the PB08 and PB09 cruises, station ALOHA (HOT program) is shown for reference. Symbols are distinguished by year (PB08, circles; PB09, squares) and bloom stations (filled symbols). Outlined regions are the maximum areal extent of the MODIS-defined bloom regions ($>0.12\ \mu g\ L^{-1}$ [Chl *a*]). Transect direction is denoted by arrows.

During PB08, a single bloom feature was sampled near the subtropical front northeast of Hawaii (Fig. 1). The bloom was intensifying as the ship left port in Hawaii and satellite chlorophyll levels were above the $0.12\ \mu g\ L^{-1}$ bloom threshold when the ship arrived at the bloom, but while the area was being sampled the satellite-observed chlorophyll levels fell below the bloom threshold. As a result of the declining biomass, only one of the 18 stations sampled in the area met the diatom-bloom criteria (Fig. 1). Two bloom features were sampled in 2009. In mid-June of 2009 a high chlorophyll feature developed east of Hawaii at ~26°N, 146°W (Fig. 1), but remotely sensed chlorophyll concentrations had dropped significantly by the time of sampling in mid-July (Fig. 1). However, satellite images revealed another bloom feature developing to the north of Hawaii at ~25°N, 155°W (Fig. 1). Two stations were sampled within this feature while it was still active (or developing), and both met the bloom-station criteria. This bloom will be referred to as the active bloom from PB09 to distinguish it from observations taken in the faded bloom further to the east.

Sampling consisted of CTD casts throughout the day. Pre-dawn casts (04:00–06:00 h, local time) were done to obtain samples for nutrient concentration, Chl *a* concentration, $bSiO_2$ concentrations and $bSiO_2$ production rates. Samples for diatom abundance and composition were taken on the rate casts or on the cast immediately before/after. On additional casts during the day, all samples were collected except those for rate measurements. Due to time constraints for sampling the second bloom region examined in 2009, rate profiles at PB09 stations 22 and 23 were conducted after 6:00 h local time, but all incubations ran 24 h to integrate through a complete photoperiod (see below). For rate measurements water samples were taken at nine depths within the euphotic zone where the percent of irradiance was determined to be 100, 59, 31, 19, 10, 6, 3.4, 0.6 and 0.1% of that just below the surface ($\%I_0$). At non-rate stations fixed sampling depths (surface: i.e. 3–5 m, 10, 20, 40, 60, 80, 100, 125, 140, 160 m) were used. Seawater was collected using 12 L PVC sampling bottles on a rosette equipped with a Seabird CTD and a photosynthetically active radiation sensor to determine light attenuation. Mixed layer depths were calculated using 1-m binned CTD data based on a $0.125\ kg\ m^{-3}$ change in potential density from the 0–1 m bin.

2.2. Nutrient, taxonomy, and biogenic particulate analysis

Dissolved nutrients were collected and analyzed using standard methods. Unfiltered seawater samples for $[Si(OH)_4]$ determination