



JGR Oceans

RESEARCH ARTICLE

10.1029/2020JC016851

Key Points:

- Phytoplankton community composition (PCC) in December 2017, during the Thomas Fire, was different from past winters in the Santa Barbara Channel (SBC)
- Many oceanographic parameters measured in the SBC varied during the Thomas Fire, but did not link directly to the fire
- While PCC varied over a week of sampling, it was ultimately uncorrelated with light, nutrients, or sea surface temperature

Supporting Information:

· Supporting Information S1

Correspondence to:

S. J. Kramer, sasha.kramer@lifesci.ucsb.edu

Citation:

Kramer, S. J., Bisson, K. M., & Fischer, A. D. (2020). Observations of phytoplankton community composition in the Santa Barbara Channel during the Thomas Fire. *Journal of Geophysical Research: Oceans*, 125, e2020JC016851. https://doi.org/10.1029/2020JC016851

Received 2 OCT 2020 Accepted 12 NOV 2020

Observations of Phytoplankton Community Composition in the Santa Barbara Channel During the Thomas Fire

Sasha J. Kramer¹, Kelsey M. Bisson², and Alexis D. Fischer³

¹Interdepartmental Graduate Program in Marine Science, University of California, Santa Barbara, Santa Barbara, CA, USA, ²Department of Botany and Plant Pathology, Oregon State University, Corvallis, OR, USA, ³Ocean Sciences Department, University of California, Santa Cruz, Santa Cruz, CA, USA

Abstract The Thomas Fire ignited on December 5, 2017 and burned nearly 300,000 acres of land in Ventura and Santa Barbara counties until January 12, 2018, making it the largest wildfire in California history at the time. During the fire, a persistent plume of ash, smoke, and soot extended up to 1,000 km offshore over the Santa Barbara Channel (SBC). The effect of this ash influx on the SBC phytoplankton community was investigated with an Imaging FlowCytobot (IFCB) onboard R/V Sally Ride during a research cruise in mid-December 2017. Over 100,000 images of phytoplankton and nonliving particles were collected and each image was manually classified, resulting in time series of phytoplankton cells and detrital particles, including ash. Comparing the Thomas Fire conditions to historical monthly sampling in the SBC in December reveals significant differences in sea surface temperature, nutrient concentration, and phytoplankton community composition (PCC) in December 2017. During the Thomas Fire, dinoflagellates dominated the phytoplankton community (comprising up to 90% of the total phytoplankton cell biovolume per sample), while diatoms and picophytoplankton typically dominate surface ocean PCC in the SBC in December. While this study was not able to demonstrate a correlational relationship between PCC and wildfire ash concentration, the significant differences in surface ocean biogeochemistry in December 2017 compared to past winters is notable. Wildfire severity and frequency are annually increasing in California and globally with unknown impacts on the marine ecosystem; thus, this study provides an important baseline assessment for the SBC.

Plain Language Summary This work describes marine phytoplankton community composition (PCC) during a wildfire. This work was conducted as part of a previously planned cruise onboard R/V Sally Ride in December 2017, which enabled us to sample PCC in the Santa Barbara Channel (SBC) during the Thomas Fire. The Thomas Fire was the largest wildfire in California history at the time, although it has since been surpassed by the Mendocino Fire complex in summer 2018 and five separate wildfires in summer 2020. This work was conducted using an Imaging FlowCytobot to quantify and characterize PCC and describe ash and detrital particle concentrations during the fire. We found that the phytoplankton community during the Thomas Fire was dominated by dinoflagellates (up to 90% of biomass), while the phytoplankton community in winter in the SBC is typically composed of diatoms or picophytoplankton. While we are not able to show a causal relationship between the Thomas Fire and PCC with the data collected on this cruise, we use time series data to show that December 2017 was significantly different from historical winters in the SBC. Warmer sea surface temperatures and a negative North Pacific Gyre Oscillation may have contributed to conditions that were favorable for dinoflagellates. Wildfire severity and frequency are expected to increase worldwide—this study provides a baseline for the impacts of wildfires in the SBC.

1. Introduction

The Thomas Fire ignited on December 5, 2017 and burned until January 12, 2018. During this time, the fire consumed nearly 300,000 acres of private, agricultural, and public land, ultimately damaging over 1,000 structures throughout Ventura and Santa Barbara Counties. At the time, the Thomas Fire became the largest fire in California's history, although it was quickly surpassed by the Mendocino Fire Complex in summer 2018 (Cal Fire; https://www.fire.ca.gov/media/5510/top20_acres.pdf) and the August Complex, SCU Lightning Complex, LNU Lightning Complex, North Complex, and Creek Fire in summer to early fall 2020 (CAL Fire, September 28, 2020; https://www.fire.ca.gov/media/11416/top20_acres.pdf). Destructive and deadly

© 2020. American Geophysical Union. All Rights Reserved.

KRAMER ET AL. 1 of 16



wildfires have increased in severity and regularity in California and other chaparral-based ecosystems in the 21st century, including recent devastating fires in Australia and Brazil. The occurrence of these fires is worsened by increased fire suppression and drought, as well as increased air temperature and dryness due to anthropogenic climate change (Abatzoglou & Williams, 2016; Doerr & Santín, 2016; Syphard et al., 2018; Westerling et al., 2006). While most of the research on these fires has been focused on the terrestrial ecosystem, little is known about impacts on the marine ecosystem, despite the occurrence of many of these fires in coastal regions. With a global increase in wildfire severity and frequency due to anthropogenic climate change, it is crucial to understand the range of consequences of wildfires on the surrounding marine environment to both better manage future coastal fires and better predict their likely impacts on coastal ocean ecosystems and economies (i.e., fisheries).

A number of previous studies have investigated the impacts of smoke and ash on aquatic ecosystems, although none have examined the impacts of wildfires on phytoplankton in marine ecosystems. Volcanic ash has been shown to have a fertilizing effect on the surface ocean, providing limiting nutrients to the existing phytoplankton community and spurring bloom conditions (Duggen et al., 2007; Hamme et al., 2010; Langmann et al., 2010; Westberry et al., 2019). The resulting phytoplankton blooms have even been hypothesized to negatively affect the surrounding ecosystem, including causing hypoxic conditions that may have led to coral reef death (e.g., Abram et al., 2003; van Woesik, 2004). Similarly, wildfires near lakes have resulted in increased chlorophyll-a concentration (which can be considered here a proxy for phytoplankton biomass), as well as measurable shifts in phytoplankton community composition (PCC) during and after a wildfire (Charette & Prepas, 2003; Planas et al., 2000). There have also been documented shifts in zooplankton diel vertical migration due to decreased light availability under thick wildfire smoke and ash, which could further alter the phytoplankton community (e.g., Urmy et al., 2016). Experimental work has considered the specific impacts of both volcanic ash and wildfire ash on phytoplankton and their production of natural products in laboratory culture experiments (e.g., Hoffmann et al., 2012; Tsai et al., 2017), while the broad effects of wildfire ash on freshwater quality and watershed ecosystems have been generally considered (e.g., Coombs & Melack, 2013).

The potential impacts of the Thomas Fire on the PCC in the SBC were completely unknown. Thus, the objective of this study was to characterize the abundance and community composition of phytoplankton in the SBC during the Thomas Fire. Based on previous work on the impacts of wildfire ash in lake ecosystems and on volcanic ash in oceanic ecosystems, it was hypothesized that the Thomas Fire and its associated smoke and ash could have either a positive or negative effect on phytoplankton biomass and PCC. Phytoplankton biomass could increase due to likely inorganic nutrient inputs from the fallout of wildfire ash on the ocean surface and associated increases in bacterial production. Alternately, phytoplankton biomass could decrease due to the decreased intensity and wavelength range of light penetrating the thick smoke overlaying the SBC.

Wildfires occur on unpredictable spatiotemporal scales, which is in direct opposition to the timeframe of oceanographic research cruises. Time onboard major research vessels is generally scheduled months to years in advance, and requires intensive planning for successful coordination. Thus, it was fortuitous that, at the time of the Thomas Fire in 2017, R/V *Sally Ride* had already been scheduled to carry a full team of scientists to the SBC from December 16 to 22 (Bisson et al., 2020). The original cruise objective was to interrogate daily variability in microbial and biogeochemical stocks and rates as part of a study named Across the Channel: Investigating Diel Dynamics (ACIDD). While many previous research programs in the SBC have measured changes in ocean biogeochemistry on monthly to seasonal time scales, ACIDD aimed to describe changes in phytoplankton, zooplankton, and bacteria on shorter (daily) time scales. However, shortly after the ignition of the Thomas Fire, sampling plans were adjusted to incorporate a direct investigation of the impacts of dry ash deposition on microbial life in the coastal ocean ecosystem. To quantify and characterize the abundance and composition of the phytoplankton community, an Imaging FlowCytobot (IFCB; Olson & Sosik, 2007; Sosik & Olson, 2007) was used during ACIDD, in addition to measurements of other relevant physical, biological, and chemical variables.

Spatiotemporal limitations in the ACIDD cruise's sampling scheme consequently limited the ability of this study to fully assess whether or not the Thomas Fire caused the observed PCC changes described in this study. Despite the relatively short occupation of the SBC, we did observe that the biological and physical

KRAMER ET AL. 2 of 16



characteristics of the surface ocean in the SBC during our week of sampling were significantly different from historical winters—notably, the PCC in December 2017 was significantly different from past winters in the SBC. Other environmental perturbations in December 2017, including strong offshore winds, make it difficult to isolate the effects of the Thomas Fire. Nevertheless, this work remains the first study to examine PCC in the coastal surface ocean during a wildfire, and therefore provides an important baseline from which to consider future impacts of wildfire ash on PCC in the SBC and beyond. We emphasize the need for sustained, long-term coastal oceanic monitoring programs, particularly in coastal regions vulnerable to unpredictable natural disasters (such as wildfires) and particularly prioritizing phytoplankton identification with high taxonomic resolution, to document future disturbances in marine ecosystems as coastal wildfires increase in frequency and severity.

2. Materials and Methods

2.1. Study Site: The Santa Barbara Channel

The SBC is located within the Southern California Bight, bounded by the mainland coast to the north and the four Northern Channel Islands to the south (Hamilton et al., 2010). Since the SBC is situated in a transition zone where three distinct water masses intersect, it is a highly variable physical, chemical, and biological environment. The cold, near-surface equator-ward California Current, the warm, salty, pole-ward Southern California Counter Current, and the deep California Undercurrent meet in the Channel to create a nearly persistent cyclonic flow (Dong et al., 2009). Wind-driven upwelling and persistent cyclonic flows allow for high nutrient concentrations through the spring to fall in the SBC, leading to high primary production and phytoplankton biomass in the surface ocean (Brzezinski & Washburn, 2011; Oey et al., 2001). Terrestrial runoff and sediment resuspension events also contribute to the seasonal and spatial patterns in nutrient concentration, light availability, and phytoplankton biomass (Otero & Siegel, 2004).

Previous work in the SBC includes the NASA-funded monthly Plumes and Blooms (PnB) time series (PnB; 1996-present), NSF-funded Santa Barbara Coastal Long-Term Ecological Research Project (SBC-LTER, 2000-present), and NOAA-funded California Cooperative Oceanographic Fisheries Investigations (Cal-COFI, 1949-present). These long-term sampling programs have surveyed optical properties, phytoplankton, zooplankton, giant kelp, fish, invertebrates, associated physical variables, inorganic nutrients, etc. PnB sampling has characterized phytoplankton abundance and community composition in the SBC using high-performance liquid chromatography (HPLC) phytoplankton pigments, which provide high information content for the cost of the measurement, but relatively low taxonomic resolution of the phytoplankton community (e.g., Anderson et al., 2008; Catlett & Siegel, 2018; Kramer & Siegel, 2019). Phytoplankton abundance in the Channel in a typical December is expected to be at its annual low (Brzezinski & Washburn, 2011), with a community of picophytoplankton or diatoms depending on nutrient availability (Anderson et al., 2008).

Finally, to assess the possibility of wind-driven upwelling in the SBC during ACIDD, regional wind forcing data were obtained from the National Data Buoy Center. Buoys 46053 (34.241°N, 119.839°W) and 46054 (34.265°N, 120.477°W) were selected, as these buoys bookend the ACIDD sampling sites.

2.2. Sampling During the Thomas Fire (December 2017)

The ACIDD cruise occurred from December 16 to 23, 2017 on R/V *Sally Ride* in the SBC (Figure 1). A broad goal of this work was to characterize the diel cycle of biological processes within the same water mass; thus, the sampling scheme followed a Lagrangian approach. Four Pacific Gyre/Mobitex "Microstar" surface drifters were deployed in a triangle or box formation at the same time, spaced 0.1–1 km apart, and the first drifter was followed for the next 24 h. Each day began with a hydrocast using the Conductivity, Temperature, and Depth (CTD) sensor at 34.25° N, 119.90°W—this location ("Station 4") has been sampled monthly with depth resolution to 500 m as part of PnB since August 1996.

CTD hydrocasts occurred every 6 hours, for a total of four hydrocasts in a 24-h cycle (Figure 1). On each CTD hydrocast, sea surface temperature (SST) was recorded and discrete samples were collected from the surface bottle (<1 m) to sample phytoplankton pigment concentration and composition, phytoplankton abundance

KRAMER ET AL. 3 of 16



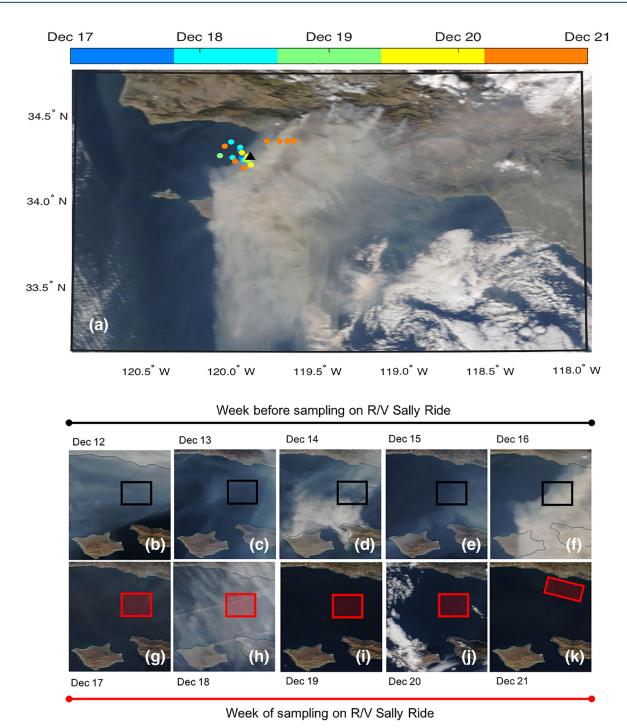


Figure 1. Map showing (a) sampling locations (colored by sampling day) overlaying MODIS Terra smoke image from December 16, 2017 and (b–k) sampling locations of R/V Sally Ride in December 2017 in for the week before sampling (black boxes) and the week of sampling (red boxes) overlaying MODIS Terra smoke image. The location of PnB Station 4 is indicated on (a) as a black triangle. We acknowledge the use of imagery from the NASA Worldview application (https://worldview.earthdata.nasa.gov), part of the NASA Earth Observing System Data and Information System.

and PCC using the IFCB, and inorganic nutrient concentrations. Samples for HPLC phytoplankton pigment analysis were collected from the surface bottles and processed at NASA's Goddard Space Flight Center by the Ocean Biology Processing Group following Van Heukelem and Thomas (2001) and Van Heukelem and Hooker (2011). Inorganic nutrient samples were taken from the same surface bottles and processed at UC Santa Barbara's analytical facility to measure the concentrations of nitrite, nitrate + nitrite, silicate, and

KRAMER ET AL. 4 of 16



phosphate ions. Photosynthetically active radiation (PAR) was collected in the visible range (400–700 nm) using the surface unit (mounted on the ship) of a Compact-Optical Profiling System (Biospherical Instruments Inc.) at 1 s resolution. PAR data were binned to 15 min average values.

2.3. Imaging Flow Cytobot (IFCB)

Phytoplankton and nonliving particles (e.g., ash and detritus) were quantified using an IFCB, an imaging-in-flow submersible cytometer that is commercially available from McLane Research Laboratories. At each sampling station, whole water samples of 50 mL were collected from the surface bottle (<1 m depth) to be imaged in triplicate by the IFCB. The IFCB collects and images a nominal 5 mL seawater sample every 25 min at a rate of up to 12 images s⁻¹. In preparation for sample intake, the whole water sample was gently resuspended to ensure it was homogeneous. During IFCB sample intake, the sample first passes through a 130 μ m Nitex screen to prevent clogging of the flow cell. The Nitex screen and the camera field of view set the effective upper size limit of cells, chains, or colonies seen in these images to length ~300 μ m. The lower size limit is set by the minimum triggering intensity needed to activate the camera and the pixel size of the camera. Particles smaller than 10 μ m were imaged, but only particles larger than 10 μ m had strong enough intensities to produce images that were visually informative. Two different triggering mechanisms were used to acquire images of phytoplankton and nonliving particles in the triplicate samples. For the first two replicates of each sample, a fluorescence trigger was used to exclusively image phytoplankton, and for the third replicate, a scattering trigger was used to image all particles. Thus, nonliving particle volume was calculated as the total particle volume less the phytoplankton biovolume.

2.4. IFCB Image Analysis

In order to quantify phytoplankton and nonliving particles from IFCB imagery, the image data set needed to be classified, either manually or using a machine learning image classifier. In an initial effort to develop a machine learning image classifier for Thomas Fire ash, dry wildfire ash was collected from a car windshield in Ventura, CA, USA on December 12, 2017 and stored in a glass jar. Dry ash was mixed with 20 mL of $0.2\,\mu m$ filtered seawater. Triplicate samples of wildfire ash mixed with filtered seawater were then analyzed on the IFCB using the scattering trigger. These samples were used to classify ash particles in natural seawater samples. Despite the large ash image training set, the images were not distinct enough from other detrital particles to successfully develop a machine learning image classifier capable of distinguishing ash from detritus. At the time of this study, a machine learning image classifier for California coastal phytoplankton did not exist. Thus, IFCB images were manually classified through an iterative process by the three authors.

Images were manually classified into 96 distinct classes based on taxonomy (phytoplankton and microzooplankton) or appearance (detritus and other nonliving particles). For the final version used in this analysis, 10 classes were selected that best represented majority of the particles in the study area: three classes of diatoms (*Chaetoceros*, all other centric diatoms, pennate diatoms), three classes of dinoflagellates (*Prorocentrum*, *Gonyaulax*, all other dinoflagellates), one class of haptophytes (*Umbilicosphaera*), the class of nanoplankton (cells <10 μ m that could not be taxonomically identified from the images), and one class of nonliving particles that included ash and detritus. The absolute abundances of cells (or chains) in these samples were determined from their apparent abundance by correcting the nominally 5 mL volume sampled to reflect the actual volume of seawater observed by the IFCB, which was always slightly less than 5 mL volume due to a short "dead time" following each trigger during which time each image is processed and stored. The morphometrics of each cell or chain were also used to determine phytoplankton biovolumes and equivalent spherical diameters (ESD) from the two-dimensional outlines in each image, using a distance map method (Moberg & Sosik, 2012). In this study, ESD is used to approximate cell and detrital particle size. Images of fluorescent microspheres of a known diameter (9 μ m, Duke Scientific Inc.) were used to provide the pixel-to-micron factor necessary to calibrate these estimated biovolumes in μ m³.

Phytoplankton class abundance and community composition measured with the IFCB were summarized using the Shannon diversity index (H), which describes the number and richness of groups sampled:

$$H = -\sum_{i=1}^{R} p_i \ln p_i$$

KRAMER ET AL. 5 of 16



Table 1							
Pearson's Correlation Coefficients (R) Between IFCB Parameters and Environmental Parameters on ACIDD							
IFCB parameter (per mL)	PAR	PO ₄ ²⁻	$NO_3^- + NO_2^{3-}$	SiO ₄ ²⁻	NH ₄ ⁺	Total chl-a	SST
Cell biovolume	-0.01	-0.49	-0.31	-0.21	0.36	0.34	0.24
Detrital particle volume	-0.13	-0.08	-0.12	-0.10	-0.19	0.08	0.22
Cell counts	-0.45	0.18	-0.01	-0.13	-0.23	-0.37	0.13
Detrital particle counts	0.06	-0.15	-0.07	-0.01	-0.06	-0.08	0.21
Median cell size	0.26	0.11	-0.07	-0.05	-0.18	-0.21	-0.44
Median detrital particle size	0.00	-0.02	-0.11	-0.11	-0.26	0.05	-0.20
Diatom counts	-0.24	-0.23	-0.20	-0.19	-0.08	0.39	-0.10
Dinoflagellate counts	0.06	-0.51	-0.31	-0.19	0.42	0.36	0.23

Note. Significant values ($p \le 0.05$) are in bold. The sign indicates the direction of the correlation.

where p_i is the proportion of individuals in the ith group identified in the data set and R is the total number of groups identified in the data set. This index describes both the richness and evenness of the community composition. Higher values of H suggest that there are both more groups represented in the data set and more members of each of those groups. A value of zero indicates only one group present in the data set.

2.5. Plumes and Blooms (PnB) Time Series Data

HPLC pigments, temperature, and nutrient concentration data collected as part of the PnB time series were used here to compare December 2017 to historical winters in the SBC. PnB has conducted approximately monthly cruises since 1996, sampling at seven stations along a ~40 km transect in the SBC (see: http://www.oceancolor.ucsb.edu/plumes_and_blooms/stations.html). In this study, data measured at PnB Station 4 (mid-channel, 34.25°N, 119.90°W) from 13 discrete winter cruises ("winter" is defined here as any cruise between December 1 and January 31; Brzezinski & Washburn, 2011) was used (data from 2005 to 2016 and 2019). The limited date range for all samples used in this analysis relative to the entire PnB time series was chosen so only HPLC samples analyzed at NASA GSFC (2005 and after) were used for this analysis. PnB methodologies have been described in detail elsewhere (e.g., Anderson et al., 2008; Catlett & Siegel, 2018). Briefly, surface seawater samples were collected for HPLC pigment and inorganic nutrient analyses from the same 5 L Niskin bottle mounted on a CTD rosette. All analyses for pigments, inorganic nutrients, and SST are identical to those described in Section 2.2 for ACIDD.

3. Results

3.1. Environmental Conditions on ACIDD (December 2017)

During the ACIDD cruise, surface chlorophyll-a concentrations in the SBC remained at a consistent low concentration of approximately 1 mg m⁻³, with the highest values of 2 mg m⁻³ measured on December 18, 2017 (Figure 2a). Total chlorophyll-a concentrations were uncorrelated with phytoplankton cell counts (Table 1; R = -0.37), detrital particle counts (R = -0.08), cell biovolume (R = 0.34), and detrital particle volume (R = 0.08). Phosphate, silicate, and nitrate + nitrite concentrations remained stable throughout the ACIDD cruise (Figure 2b). Nitrate + nitrite and silicate were not significantly correlated with phytoplankton and detrital particle abundance and biovolume, but phosphate was significantly negatively correlated with both cell biovolume and dinoflagellate cell concentration (Table 1; R = -0.49 and -0.51, p = 0.02 and 0.01, respectively). Quarter-hourly averaged PAR varied as expected on daily timescales with hourly variability in intensity that can likely be attributed to the variability in smoke and ash cover over the SBC (Figure 2c). The nearest quarter-hourly averaged PAR value was matched to each CTD sample to determine a correlation with IFCB properties. PAR was significantly negatively correlated with IFCB cell counts (R = -0.45, p = 0.04). Finally, SST was relatively stable throughout the cruise, varying less than 1 degree (Figure 2d). SST was negatively correlated with median cell size (Table 1; R = -0.44, p = 0.03), suggesting

KRAMER ET AL. 6 of 16

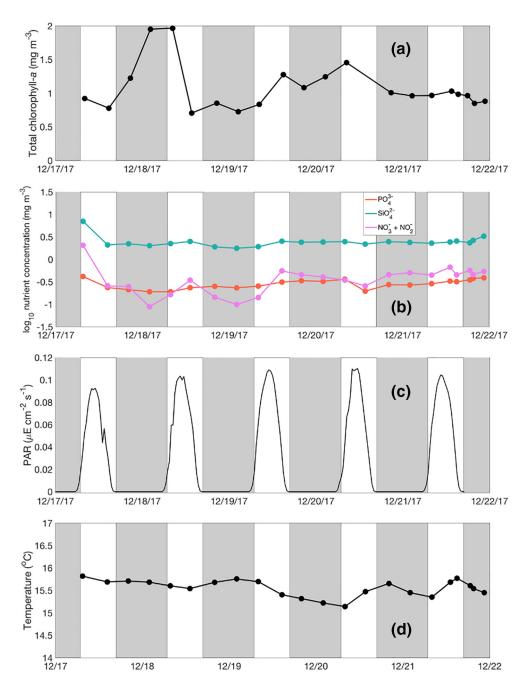


Figure 2. Time series of surface measurements of (a) total chlorophyll-a from HPLC, (b) log transformed inorganic nutrients (orange = phosphate $[PO_4^{3-}]$, teal = silicate $[SiO_4^{2-}]$, pink = nitrate $[NO_3^{-}]$ + nitrite $[NO_2^{-}]$), (c) photosynthetically active radiation (PAR), and (d) sea surface temperature.

that there was some correlation within this small range of temperature favoring smaller cell sizes at higher temperatures, and vice versa.

In the 2 weeks before and during the ACIDD sampling period, regional winds impacting the western and eastern sides of the SBC were observed at buoys 46054 and 46053, respectively. During ACIDD at buoy 46054, winds blew strongly from the northwest, and these winds weakened and changed to blowing primarily from the west as they moved across the channel to buoy 46053 (Figure S1). West and northwest winds indicate the absence of upwelling-favorable conditions.

KRAMER ET AL. 7 of 16

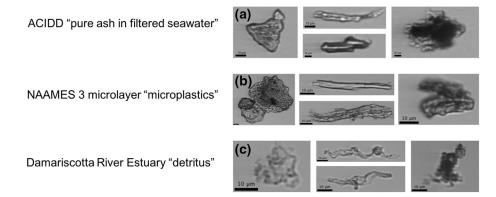


Figure 3. Example IFCB images of (a) pure ash in filtered seawater (ACIDD), (b) microplastics and fibers (NAAMES 3 microlayer, https://ecotaxa.obs-vlfr.fr/prj/642), and (c) detritus (Damariscotta River Estuary, https://ecotaxa.obs-vlfr.fr/prj/799).

3.2. Ash Particle Classification

IFCB images of dry ash in filtered seawater were used to describe and quantify natural ash particles in the ocean during ACIDD. The dry ash sample was composed of particles with variable size, shape, and color (Figure 3a). Despite the large number of IFCB images obtained during this experimental work with dry ash, the images of ash particles were not distinct enough from other detrital particles to create a machine learning image classifier to distinguish ash from detritus. Instead, images of the dry ash sample looked remarkably similar to other detrital particles in seawater imaged with the IFCB, including microplastics imaged in the North Atlantic Ocean as part of NASA's North Atlantic Aerosols and Marine Ecosystems Study (NAAMES; Figure 3b) and detrital particles imaged in the Damariscotta River Estuary in Maine, USA (Figure 3c). Local wildfires were not present during either example. Due to the similarity between IFCB images of ash, microplastics, and detritus, we chose to count ash and detritus particles together during ACIDD (henceforth in this analysis, "detritus" includes both ash and other detrital particles).

3.3. Cell and Detrital Particle Characteristics

The number, volume, and size of both cells and detrital particles varied throughout the week of sampling during the ACIDD cruise (Figure 4). The highest number and total volume of detrital particles occurred on December 18, 2017 (Figures 4a and 4b). This relative maximum was characterized by smaller detritus particles of around 8.5 μ m; the maximum mean detrital particle size of 11 μ m occurred on December 20, 2017 (Figure 4c). One major peak in cell biovolume per sample volume occurred on the cruise, on December 18, 2017 (Figure 4a). However, relative maxima in cell counts on the cruises did not align with maxima in cell biovolume: the maximum number of cells per sample volume were found on December 18, 19, and 21, 2017 (Figure 4b). Finally, the mean cell size was consistently between 7 and 8 μ m, with a relative maximum of 8.5 μ m cells on December 19, 2017 (Figure 4c).

Phytoplankton cell biovolume per sample volume was consistently 2 orders of magnitude higher than detrital particle volume per sample volume during the Thomas Fire (Figure 4a). Cell concentrations were also almost always higher than detrital particle concentrations (Figure 4b). However, the median size of detrital particles was generally larger than the median cell size during the Thomas Fire by $\sim 1~\mu m$.

3.4. Phytoplankton Community Composition

Phytoplankton comprised between 25% and 90% of the total particle volume on ACIDD (Figure 5a), while detritus particles comprised between 10% and 75% of the total particle volume for a given sample. Within the phytoplankton fraction, IFCB imagery also allowed for characterization of the PCC during the Thomas Fire to relatively high taxonomic resolution (typically genus to species level). Most of the cells imaged

KRAMER ET AL. 8 of 16

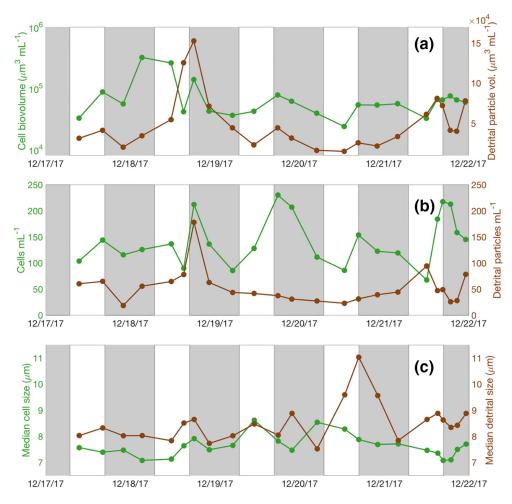


Figure 4. Time series of (a) cell biovolume and detrital particle volume concentrations, (b) cell and detrital particle concentrations, and (c) median equivalent spherical diameters of cells and detrital particles. The color green indicates cells and brown indicates detritus. Shaded bars indicate nighttime (sunset and sunrise) on the day of sampling.

during ACIDD in a given sample were nanoplankton (6%–70%) and dinoflagellates (5%–90%) with a smaller fraction of the community composed of diatoms (1%–25%) or other phytoplankton (1%–20%) not described in these general groups (Figure 5b). The dinoflagellate fraction on ACIDD was mostly composed of members of *Prorocentrum* and *Gonyaulax* genera (Figure 5c). The majority of diatoms imaged were centric species (Figure 5c). The coccolithophore genus *Umbilicosphaera* comprised 2%–10% of the total biovolume in nearly all samples from ACIDD.

On the ACIDD cruise, specific phytoplankton groups rapidly increased in measured abundance and then either decreased or vanished completely on daily timescales (Figure 6). The dinoflagellate genera *Gonyaulax* and *Prorocentrum* experienced marked increases in cell concentration on December 18 and 19, 2017, respectively. While the coccolithophore genus *Umbilicosphaera* did not reach the same cell abundances in the surface ocean during ACIDD as the dinoflagellate genera, this group was consistently counted at low levels in nearly all samples.

The Shannon diversity index (**H**) on ACIDD was typically between 0.40 and 1.00, with the exception of December 17–18, 2017, when the **H** value was 1.73–1.86 (Figure 7). On these days, the IFCB imagery showed a peak in *Prorocentrum* cell abundance (Figure 6), as well as contributions to total cell biovolume by many other groups including nanoplankton, diatoms, other dinoflagellates, and *Umbilicosphaera* cells. The relatively high value of **H** suggests that both the overall number of phytoplankton groups and the cell counts of most of these phytoplankton group were high on these dates.

KRAMER ET AL. 9 of 16

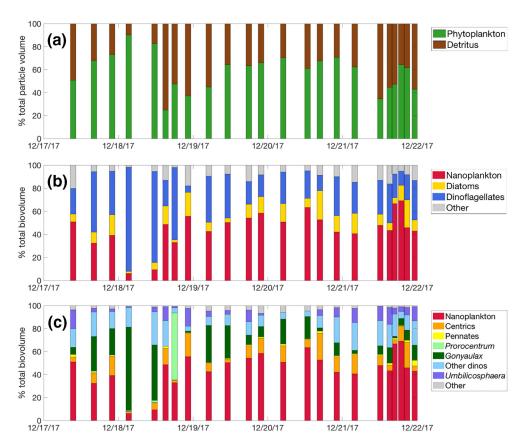


Figure 5. Time series of (a) total phytoplankton and detrital particle volume fractions, (b) phytoplankton phylum-specific biovolume fractions, (c) phytoplankton genus-specific biovolume fractions.

3.5. Comparing December 2017 to Historical Winters in the SBC

The PnB data set provided over a decade of historical data from the SBC with which to compare the surface ocean biogeochemistry on the ACIDD cruise (Figure 8). While the mean chlorophyll-*a* concentration measured on ACIDD was consistent with the average chlorophyll-*a* in a typical winter in the SBC (Figure 8a), the PCC and physicochemical conditions underlying that chlorophyll-*a* concentration were quite different. Fucoxanthin (a biomarker pigment found mainly in diatoms, but also many other taxonomic groups) was significantly lower in December 2017 compared to historical winters (Figure 8b). Meanwhile, peridinin (a biomarker pigment found in most, but not all, dinoflagellates) was found in higher concentrations on ACIDD than in the average winter in the SBC (Figure 8c).

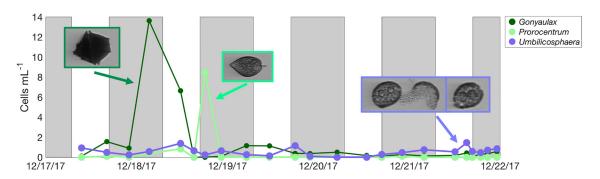


Figure 6. Time series of prevalent genera during ACIDD: Gonyaulax (dark green), Prorocentrum (light green), and Umbilicosphaera (purple).

KRAMER ET AL. 10 of 16

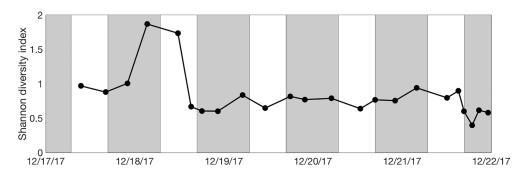


Figure 7. Shannon diversity index for all surface samples. Higher numbers indicate higher evenness and/or diversity of species.

There was significantly less nitrate in the surface water in December 2017 (Figure 8d; t-test, p < 0.05), but similar concentrations of phosphate (data not shown), leading to lower-than-average nitrogen to phosphorus (N:P) ratios (Figure 8e). Finally, though the SST was relatively invariant on ACIDD (Figure 2d), this narrow range of temperatures was significantly warmer than what would be expected of a typical winter in the SBC (t-test, p < 0.05). Unfortunately, equivalent historical PAR measurements in the SBC were not available for comparison to December 2017.

4. Discussion

This study characterized the PCC and detrital particle dynamics in the SBC during the Thomas Fire, and compared the surface ocean biogeochemistry during the fire to historical winters in the SBC. Although chlorophyll-a concentration was not significantly different in December 2017 compared to historical winters (Figure 8a), the PCC underlying the chlorophyll-a signal was quite different. Our results show high variability in PCC and cell abundance and detrital particle concentration throughout the week of sampling

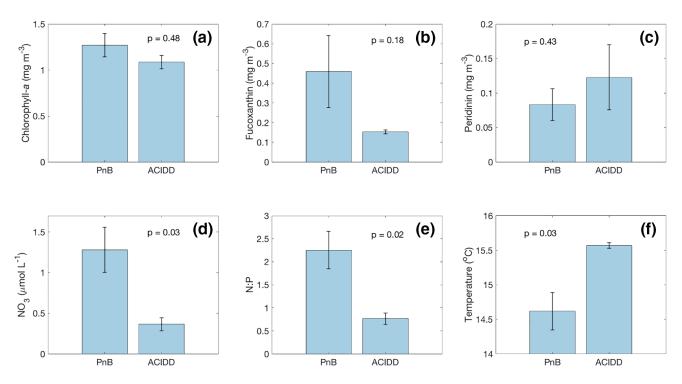


Figure 8. Comparison of winter (December 1 to January 31) Plumes and Blooms values (13 cruises between 2005 and 2019) and December 2017 values of (a) total chlorophyll-*a*, (b) fucoxanthin, (c) peridinin, (d) nitrate (NO₃), (e) nitrogen to phosphorus (N:P), and (f) temperature. *p* Values are indicated on each plot; values < 0.05 are considered significant.

KRAMER ET AL. 11 of 16



during the Thomas Fire. Both IFCB imagery and HPLC pigments confirm the presence of an unusually high number of dinoflagellates in the SBC on ACIDD. Conversely, in past winters, diatoms and picophytoplankton were observed in high abundance in the SBC. The surface ocean was unusually warm on ACIDD compared to a typical winter in the SBC (Figure 8f), while surface nitrate concentrations were significantly lower than expected based on historical sampling (Figure 8d).

4.1. Impacts of the Thomas Fire on PCC

Before the ACIDD cruise, it was hypothesized that the impacts of the Thomas Fire on the environment surrounding the SBC could lead to perhaps mixed effects on phytoplankton abundance and community composition. On one hand, the fire caused deposition of wildfire ash on the surface ocean, with the potential to increase bacterial activity in the surface ocean and provide bioavailable inorganic nutrients that could stimulate phytoplankton growth. On the other hand, the smoke and ash in the sky above the SBC could have reduced the PAR (limiting phytoplankton growth) and/or reduced the UV light (limiting diel vertical migration by zooplankton and thus decreasing grazing of the phytoplankton community) reaching the surface ocean. While the samples collected on ACIDD are not sufficient to demonstrate a correlational or causal relationship between smoke and ash concentrations and PCC, the phytoplankton community in December 2017 was notably different from the expected community in winter in the SBC.

Did the Thomas Fire influence the biogeochemistry of the surface ocean in the SBC? The results of this work are inconclusive. The inorganic nutrients measured during ACIDD did not vary throughout the week of sampling (Figure 2b). Phosphate was negatively correlated with cell biovolume and dinoflagellate cell counts (Table 1), but is not expected to be a limiting nutrient in this environment, so the drawdown of phosphorus with the increase in phytoplankton biovolume (which was dominated by dinoflagellates) is not surprising. Nitrate was lower than expected in the SBC in winter (Figures 8d and 8e), but did not appear to limit growth during our period of sampling, given the consistent chlorophyll-a concentration measured on ACIDD compared to historical winters (Figure 8a). Similarly, it was hypothesized that strong offshore Santa Ana winds during the Thomas Fire may have enhanced coastal upwelling in the SBC, which would also provide a source of inorganic nutrients to the surface ocean (e.g., Fovell & Gallagher, 2018; Guzman-Morales & Gershunov, 2019). The relatively invariant SSTs during the week of sampling suggest that, if there was an upwelling event due to the strengthened Santa Ana winds during the Thomas Fire, it did not occur during the week of ACIDD sampling in mid-December 2017 (Figure 2d). Further, the wind speed and direction during the week of sampling do not suggest conditions favorable to upwelling (Figure S1). Upwelling in the SBC requires eastward winds (Brzezinski & Washburn, 2011), while the winds measured at two buoys in the SBC on December 17-21, 2017 were predominantly west and northwest.

It was also hypothesized that the thick layer of smoke and ash over the SBC could potentially limit the PAR reaching the surface ocean (Figure 1), leading to decreased capacity for photosynthesis and phytoplankton growth. The consistent values of PAR (Figure 2c) and lack of correlation between PAR and parameters measured by the IFCB (Table 1, Pearson's correlation coefficient [R] ranging from -0.45 to 0.26) suggest otherwise. In the absence of bottom-up (e.g., nutrient limiting) conditions impacting PCC, top-down controls were considered. While PAR was unaffected, it is possible that light was limited in the UV range. Urmy et al. (2016) and Rose et al. (2009) found that PAR was unaffected from wildfire smoke in the surface of an oligotrophic lake, but the UV range was significantly limited. Urmy et al. (2016) demonstrate the impact of this reduced UV range on the diel vertical migration of zooplankton. It is likely that this same decrease in UV light occurred during the Thomas Fire, suggesting that the grazing behavior of zooplankton could have been altered, which would have exerted top-down pressure on the phytoplankton community that may have influenced PCC. While the data collected on ACIDD are insufficient to provide a clear correlational relationship between the hypothesized effects of the fire and the resulting PCC in the surface ocean, this study has demonstrated that the biogeochemical conditions on the ACIDD cruise contrasted significantly with the expected conditions for winters in the SBC. It is also possible that a more significant bottom-up effect occurred outside of our sampling window, as the ACIDD cruise only captured 1 week in December 2017.

The results presented here show that the phytoplankton community measured on ACIDD was characterized by an unusually high dinoflagellate cell abundance (Figures 4 and 5). The methods used in this study were different than previous methods used to characterize the phytoplankton community in the

KRAMER ET AL. 12 of 16



SBC. Pigment-based phytoplankton taxonomy has been characterized in the SBC as part of PnB for decades (Anderson et al., 2008; Catlett & Siegel, 2018; Catlett et al., 2019). Fucoxanthin (a biomarker pigment for diatoms) on ACIDD is on the low range of PnB values (Figure 8b), while peridinin (a biomarker pigment for some dinoflagellates) on ACIDD was higher than on any PnB cruise since 2005 (Figure 8c). The PnB historical monthly HPLC pigment record suggests that the phytoplankton community in December is typically dominated by diatoms or composed of a mixture of picophytoplankton and cyanobacteria. However, anomalous dinoflagellate blooms have previously occurred in the SBC in December during the PnB time series, specifically during conditions of high nutrient input from elevated stream runoff (Anderson et al., 2008; Otero & Siegel, 2004). The relatively high Shannon index throughout the week of sampling on ACIDD (Figure 7) suggests that dinoflagellates did not unilaterally dominate the PCC in the surface ocean. Many other phytoplankton groups and species, particularly nanosized cells, were still found in high concentrations during ACIDD, though dinoflagellates comprised a high fraction of the sample biovolume in most samples (Figure 5).

This unusual presence of dinoflagellates in the SBC during the ACIDD cruise (Figures 8b and 8c) could be attributed to a number of factors, acting either individually or together. The first possibility is that the related impacts of the Thomas Fire created conditions favorable to dinoflagellate growth. The ability of dinoflagellate species to thrive despite intense environmental disturbance, including toxic pollution, has been well documented (e.g., Pospelova et al., 2002). Residual populations of dinoflagellates may have been present before the fire, or dinoflagellate populations may have been physically transported into the SBC (Catlett et al., 2019) and responded positively to any environmental disruption caused by the fire. It is also possible that the dinoflagellate dominance in the SBC in December 2017 may have been associated with regional and basin-scale oceanographic variability observed in the California Current System, independent of (or concurrent with) the impacts of the Thomas Fire. In December 2017, anomalously warm SSTs were observed throughout the California Current System and the North Pacific Gyre Oscillation was strongly negative, at –2.69 (Barth et al., 2020; Di Lorenzo et al., 2008; Fischer et al., 2020). These oceanographic anomalies were associated with an extended increase in dinoflagellate abundance in Monterey Bay (Fischer et al., 2020) and San Luis Obispo Bay (Barth et al., 2020) from 2017 to 2018. It is likely that these conditions similarly impacted the phytoplankton community in the SBC.

4.2. Strengths and Limitations of the IFCB to Describe Phytoplankton and Detritus

The use of the IFCB in this study enhanced quantification and characterization of the PCC in the SBC during and after the Thomas Fire (Figures 4 and 5). The IFCB allows for faster and often more accurate characterization of the phytoplankton community than traditional light microscopy (Sosik & Olson, 2007) and at much higher taxonomic resolution than HPLC pigments used in the historical PnB monthly sampling record, although there is often reasonably good agreement between these two measurement types (e.g., Kramer et al., 2018). The higher-than-average concentration of peridinin found on ACIDD (Figure 8c) confirms that the presence of the dinoflagellates imaged by the IFCB would still have appeared in a pigment-based record. The IFCB is limited to characterizing particles within a certain size range—however, future work with this data set will integrate other concurrent measurements from ACIDD of phytoplankton size and community composition (including flow cytometry and 18S DNA metabarcoding) to better describe the fraction of phytoplankton cells <6 µm. Two of the most abundant dinoflagellate genera imaged during ACIDD were Gonyaulax and Prorocentrum; both groups are known to have toxic or harmful member species (e.g., Vernet et al., 1989). While manual annotation of IFCB images could provide taxonomic information to the genus level, it is impossible to know if the imaged cells were toxic or harmful species. Despite these limitations, the IFCB provided measurements of the phytoplankton community in the SBC at unprecedented taxonomic resolution, compared to previous analyses that have used HPLC pigments to achieve coarser taxonomic resolution (Anderson et al., 2008; Catlett & Siegel, 2018; Kramer & Siegel, 2019).

The IFCB was also crucial to quantify and describe detrital particles both experimentally and in natural samples. While the similarity of the ash particles to microplastics and detritus made it impossible to separate ash from detritus in our analyses (Figure 3), our use of the IFCB to describe nonliving particles allowed for comparison of the fluctuating abundance, volume, and size of detrital particles, including ash particles, during the Thomas Fire. The record of detrital and ash particles in the surface ocean measured here by the

KRAMER ET AL. 13 of 16



IFCB shows the variability in particle deposition over the course of a week (Figure 4). The IFCB imagery together with satellite imagery of smoke over the SBC shows the high variability in smoke (and, presumably, ash deposition over the SBC) on each day before and during the December 2017 sampling (Figures 1b–1k). However, variability in smoke could not be detected by changes in PAR, which is consistent with other studies that have examined the impact of wildfire smoke on surface PAR (e.g., Rose et al., 2009; Urmy et al., 2016). Both the number and size of detrital particles varied over time, likely indicating changing intensity in wind direction and speed during this time (Figure S1; Fovell & Gallagher, 2018; Guzman-Morales & Gershunov, 2019). While optical proxies were measured during the fire to describe the concentration and relative size of particles, including detritus, in the surface ocean, the IFCB allowed for exact quantification and characterization of these particles through imagery. While detritus can have many different sources in the ocean, including phytoplankton bloom decline, the satellite imagery of smoke over the SBC before and during the time of sampling allows for further speculation as to the source of these particles.

4.3. The Challenge and Importance of Characterizing the Impact of Wildfires on the Ocean

Previous work describing the impact of smoke and ash on aquatic ecosystems has either focused on volcanic ash and lava in the ocean (e.g., Duggen et al., 2007; Hamme et al., 2010; Hoffmann et al., 2012; Wilson et al., 2019) or wildfire ash on boreal lakes (e.g., Charette & Prepas, 2003; Planas et al., 2000) and coral reefs (e.g., Abram et al., 2003). The work completed on ACIDD provides the first measurements of the nearshore surface ocean phytoplankton community during a wildfire on land. However, the sample collection was serendipitous: if not for a previously planned research cruise in the SBC, the ACIDD expedition would never have been able to take advantage of the unique sampling opportunity provided to investigate the impacts of a wildfire on the ocean. Given the expense and planning required for any major oceanographic research cruise, this sampling opportunity represented a rare opportunity to sample the coastal surface ocean during a wildfire.

While other groups in Southern California sampled the surface ocean and atmosphere during the Thomas Fire, their samples did not include characterizations of the phytoplankton community and had a sampling duration of just one day (Seth John, personal communication). Given the increasing frequency of wild-fires in coastal regions (including but not limited to the western United States, Australia, and Spain), it is essential to describe the impacts of these events on the oceans (Doerr & Santín, 2016). As phytoplankton serve as the base of the marine food web and a major component of the biological carbon pump, the impact of wildfires on phytoplankton abundance and community composition could have a cascading effect on the ecosystem and biogeochemistry throughout the duration of the fire. Sampling during unpredictable environmental disasters, such as wildfires, favors established coastal ocean time series observatories. The monthly PnB sampling in the SBC provides a snapshot of the conditions in a highly variable region; the week of intensive sampling on ACIDD shows just how quickly the PCC is changing on hourly to daily time scales. Conversely, a continuous monitoring system (e.g., the IFCB moored on Santa Cruz Municipal Wharf; Fischer et al., 2020) would allow for comparison of the PCC before, during, and after the ignition of a coastal wildfire in the study region. As these coastal wildfire events increase in frequency and severity, sustained monitoring will be more important than ever to capture the impacts of wildfires on the ocean.

The results presented here suggest that the environmental conditions co-occurring with the Thomas Fire in December 2017 created conditions that were favorable for an unusual, and potentially harmful, phytoplank-ton community in the SBC. Though the data collected on ACIDD were insufficient to prove a correlational relationship between wildfire ash and PCC, as might have been hypothesized from first principles, this work demonstrated that December 2017 was significantly different from previous winters in the SBC, likely influenced by the anomalously high SST and strongly negative NPGO. While this study provides a baseline for the SBC during one wildfire, without more work to characterize the broader impact of wildfires on the ocean, it will be impossible to know if these results are consistent between other wildfires and other coastal marine ecosystems. Long-term monitoring becomes particularly important during an ecological disaster to provide a benchmark against which to consider environmental change. The serendipity of this sampling opportunity underlines the importance of emergency funding for oceanographic fieldwork during disasters, such as wildfires, which are expected to increase in frequency and severity with worsening anthropogenic climate change (e.g., Doerr & Santín, 2016).

KRAMER ET AL. 14 of 16



Data Availability Statement

All ACIDD IFCB images used in this study are available online at the Kudela Lab IFCB dashboard: http://128.114.25.154:8888/ACIDD. ACIDD HPLC pigment data and nutrient data are available through NASA's SeaBASS data repository: https://seabass.gsfc.nasa.gov/cruise/ACIDD_2017. ACIDD sea surface temperature and other ship-related data are available through R2R repository: https://www.rvdata.us/search/cruise/SR1718. Plumes and Blooms HPLC data are also available through SeaBASS: https://seabass.gsfc.nasa.gov/experiment/Plumes_and_Blooms. Plumes and Blooms nutrient and SST data are available via UCSB servers (http://www.oceancolor.ucsb.edu/plumes_and_blooms/).

Acknowledgments

The University of California's Ship Funds Program, the National Academies Keck Futures Initiative, UCSB's Coastal Fund, NASA grant #NNX-17AK04G, and NSF grant #1821916 provided funding for this project. The IFCB used in this study was supported by NOAA through a grant from the Marine Sensors Technology Transition program (NA14NOS0120148) to Raphael Kudela at the University of California Santa Cruz, S. J. Kramer is supported by a National Defense Science and Engineering Graduate (NDSEG) fellowship through the Office of Naval Research. A. D. Fischer was supported by a California Sea Grant Delta Science Postdoctoral Fellowship (SEAAF18/ 182GEA/416723/440000). This work could not have been accomplished without the enthusiastic support of the Captain and crew of R/V Sallv Ride and all other members of the ACIDD science team. We are grateful for support from Raphael Kudela-without his generosity and willingness to lend his IFCB to our project, this work would not have been possible. We are especially thankful to Miranda, for everything. Thank you to Crystal Thomas at NASA GSFC for processing the ACIDD and PnB HPLC samples with high precision and accuracy. Thank you also to Paula Bontempi, Laura Lorenzoni, and Ivona Cetinić who facilitated running the ACIDD HPLC samples at NASA GSFC. Conversations with Ali Chase. Nils Haëntjens, Heidi Sosik, Seth John and his group at USC, Amir Ibrahim, and Anna McGaraghan were crucial to the completion of this work. Thank you to Nick Nidzieko, Ellie Arrington, Schuyler Nardelli, Margaret Lindeman, and Kate Nesbit for IFCB and ash sampling support. We are also grateful for sustained support from Dave Siegel, Emmanuel Boss, and Mike Behrenfeld. Two anonymous reviewers greatly improved the content and quality of this manuscript. We are also grateful to the editor, Dr. Peter Brewer, whose suggestions and encouragement saw this manuscript through to publication.

References

- Abatzoglou, J. T., & Williams, A. P. (2016). Impact of anthropogenic climate change on wildfire across western US forests. *Proceedings of the National Academy of Sciences of the United States of America*, 113(42), 11770–11775. https://doi.org/10.1073/pnas.1607171113
- Abram, N. J., Gagan, M. K., McCulloch, M. T., Chappell, J., & Hantoro, W. S. (2003). Coral reef death during the 1997 Indian Ocean dipole linked to Indonesian wildfires. *Science*, 301(5635), 952–955. https://doi.org/10.1126/science.1083841
- Anderson, C. R., Siegel, D. A., Brzezinski, M. A., & Guillocheau, N. (2008). Controls on temporal patterns in phytoplankton community structure in the Santa Barbara Channel, California. *Journal of Geophysical Research*, 113(C04038), 1–16. https://doi.org/10.1029/2007JC004321
- Barth, A., Walter, R. K., Robbins, I., & Pasulka, A. (2020). Seasonal and interannual variability of phytoplankton abundance and community composition on the Central Coast of California. *Marine Ecology Progress Series*, 637, 29–43. https://doi.org/10.3354/meps13245
- Bisson, K. M., Baetge, N., Kramer, S. J., Catlett, D., Girling, G., McNair, H., et al. (2020). California wildfire burns boundaries between science and art. *Oceanography*, 33(1), 16–19. https://doi.org/10.5670/oceanog.2020.110
- Brzezinski, M. A., & Washburn, L. (2011). Phytoplankton primary productivity in the Santa Barbara Channel: Effects of wind driven upwelling and mesoscale eddies. *Journal of Geophysical Research*, 116(C12), 1–17. https://doi.org/10.1029/2011JC007397
- Catlett, D. S., & Siegel, D. A. (2018). Phytoplankton pigment communities can be modeled using unique relationships with spectral absorption signatures in a dynamic coastal environment. *Journal of Geophysical Research: Oceans*, 123, 246–264. https://doi.org/10.1002/2017JC013195
- Catlett, D. S., Simons, R., Guillocheau, N., Henderikx-Freitax, F., & Siegel, D. A. (2019). Seasonal to decadal scale phytoplankton functional type dynamics in the Santa Barbara Channel. Oral presentation at the 2019 Eastern Pacific Ocean Conference. Retrieved from https://drive.google.com/file/d/1bUUHrbHJArCuSr-MQvnRQok7M_yTHR5G/view
- Charette, T., & Prepas, E. E. (2003). Wildfire impacts on phytoplankton communities of three small lakes on the Boreal Plain, Alberta, Canada: A paleolimnological study. Canadian Journal of Fisheries and Aquatic Sciences, 60, 584–593. https://doi.org/10.1139/F03-049
- $Coombs, J. \, S., \, \& \, Melack, J. \, M. \, (2013). \, Initial \, impacts \, of \, a \, wild fire \, on \, hydrology \, and \, suspended \, sediment \, and \, nutrient \, export \, in \, California \, chaparral \, watersheds. \, \\ \textit{Hydrological Processes}, \, 27, \, 3842-3851. \, \\ \textit{https://doi.org/10.1002/hyp.9508}$
- Di Lorenzo, E., Schneider, N., Cobb, K. M., Chhak, K., Franks, P. J. S., Miller, A. J., et al. (2008). North Pacific Gyre Oscillation links ocean climate and ecosystem change. *Geophysical Research Letters*, 35(8), 1–6. https://doi.org/10.1029/2007GL032838
- Doerr, S. H., & Santín, C. (2016). Global trends in wildfire and its impacts: Perceptions versus realities in a changing world. *Philosophical Transactions of the Royal Society B*, 371, 1–10. https://doi.org/10.1098/rstb.2015.0345
- Dong, C., Idica, E. Y., & McWilliams, J. C. (2009). Circulation and multiple-scale variability in the Southern California Bight. *Progress in Oceanography*, 82(3), 168–190. https://doi.org/10.1016/j.pocean.2009.07.005
- Duggen, S., Croot, P., Schacht, U., & Hoffmann, L. (2007). Subduction zone volcanic ash can fertilize the surface ocean and stimulate phytoplankton growth: Evidence from biogeochemical experiments and satellite data. *Geophysical Research Letters*, 34, 1–5. https://doi.org/10.1029/2006GL027522
- Fischer, A. D., McGaraghan, A., Hayashi, K., & Kudela, R. M. (2020). Return of the "age of dinoflagellates": Drivers of unusual dinoflagellate dominance in northern Monterey Bay examined using automated imaging flow cytometry. *Limnology and Oceanography*, 65, 2125–2141. https://doi.org/10.1002/lno.11443
- Fovell, R. G., & Gallagher, A. (2018). Winds and gusts during the Thomas fire. Fire, 1(47), 1–22. https://doi.org/10.3390/fire1030047
- Guzman-Morales, J., & Gershunov, A. (2019). Climate change suppresses Santa Ana winds of Southern California and sharpens their seasonality. *Geophysical Research Letters*, 46, 2772–2780. https://doi.org/10.1029/2018GL080261
- Hamilton, S. L., Caselle, J. E., Malone, D. P., & Carr, M. H. (2010). Incorporating biogeography into evaluations of the Channel Islands marine reserve network. Proceedings of the National Academy of Sciences of the United States of America, 107(43), 18272–18277. https://doi.org/10.1073/pnas.0908091107
- Hamme, R. C., Webley, P. W., Crawford, W. R., Whitney, F. A., DeGrandpre, M. D., Emerson, S. R., et al. (2010). Volcanic ash fuels anomalous plankton bloom in subarctic Northeast Pacific. *Geophysical Research Letters*, 37, 1–5. https://doi.org/10.1029/2010GL044629
- Hoffmann, L. J., Breitbarth, E., Ardelan, M. V., Duggen, S., Olgun, N., Hassellöv, M., & Wängberg, S.-Å. (2012). Influence of trace metal release from volcanic ash on growth of *Thalassiosira pseudonana* and *Emiliania huxleyi*. *Marine Chemistry*, 132, 28–33. https://doi.org/10.1016/j.marchem.2012.02.003
- Kramer, S. J., Roesler, C. S., & Sosik, H. M. (2018). Bio-optical discrimination of diatoms from other phytoplankton in the surface ocean: Evaluation and refinement of a model for the Northwest Atlantic. Remote Sensing of Environment, 217, 126–143. https://doi. org/10.1016/j.rse.2018.08.010
- Kramer, S. J., & Siegel, D. A. (2019). How can phytoplankton pigments be best used to characterize surface ocean phytoplankton groups for ocean color remote sensing algorithms? *Journal of Geophysical Research: Oceans*, 124, 7557–7574. https://doi.org/10.1029/2019JC015604
 Langmann, B., Zakšek, K., Hort, M., & Duggen, S. (2010). Volcanic ash as fertiliser for the surface ocean. *Atmospheric Chemistry and Physics*, 10, 3891–3899. https://doi.org/10.5194/acp-10-3891-2010
- Moberg, E. A., & Sosik, H. M. (2012). Distance maps to estimate cell volume from two-dimensional plankton images. *Limnology and Oceanography: Methods*, 10, 278–288. https://doi.org/10.4319/lom.2012.10.278.
- Oey, L. Y., Wang, D. P., Hayward, T., Winant, C., & Hendershott, M. (2001). "Upwelling" and "cyclonic" regimes of the near-surface circulation in the Santa Barbara Channel. *Journal of Geophysical Research*, 106(C5), 9213–9222. https://doi.org/10.1029/1999JC000129

KRAMER ET AL. 15 of 16



- Olson, R. J., & Sosik, H. M. (2007). A submersible imaging-in-flow instrument to analyze nano- and microplankton: Imaging FlowCytobot. Limnology and Oceanography: Methods, 5, 195–203. https://doi.org/10.4319/lom.2007.5.195
- Otero, M. P., & Siegel, D. A. (2004). Spatial and temporal characteristics of sediment plumes and phytoplankton blooms in the Santa Barbara Channel. Deep-Sea Research Part II: Topical Studies in Oceanography, 51, 1129–1149. https://doi.org/10.1016/j.dsr2.2004.04.004
- Planas, D., Desrosiers, M., Groulx, S.-R., Paquet, S., & Carignan, R. (2000). Pelagic and benthic algal responses in eastern Canadian Boreal Shield lakes following harvesting and wildfires. Canadian Journal of Fisheries and Aquatic Sciences, 57, 136–145. https://doi.org/10.1139/f00-130
- Pospelova, V., Chmura, G. L., Boothman, W. S., & Latimer, J. S. (2002). Dinoflagellate cyst records and human disturbance in two neighboring estuaries, New Bedford Harbor and Apponagansett Bay, Massachusetts (USA). *The Science of the Total Environment*, 298, 81–102. https://doi.org/10.1016/S0048-9697(02)00195-X
- Rose, K. C., Williamson, C. E., Schladow, S. G., Winder, M., & Oris, J. T. (2009). Patterns of spatial and temporal variability of UV transparency in Lake Tahoe, California-Nevada. *Journal of Geophysical Research*, 114, G00D03. https://doi.org/10.1029/2008JG000816
- Sosik, H. M., & Olson, R. J. (2007). Automated taxonomic classification of phytoplankton sampled with imaging-in-flow cytometry. Limnology and Oceanography: Methods, 5, 204–216. https://doi.org/10.4319/lom.2007.5.204
- Syphard, A. D., Brennan, T. J., & Keeley, J. E. (2018). Drivers of chaparral type conversion to herbaceous vegetation in coastal Southern California. *Diversity and Distributions*, 25, 90–101. https://doi.org/10.1111/ddi.12827
- Tsai, K.-P., Uzun, H., Karanfil, T., & Chow, A. T. (2017). Dynamic changes of disinfection byproduct precursors following exposures of Microcystis aeruginosa to wildfire ash solutions. Environmental Science and Technology, 51, 8272–8282. https://doi.org/10.1021/acs.est 7b01541
- Urmy, S. S., Williamson, C. E., Leach, T. H., Schladow, S. G., Overholt, E. P., & Warren, J. D. (2016). Vertical redistribution of zooplankton in an oligotrophic lake associated with reduction in ultraviolet radiation by wildfire smoke. *Geophysical Research Letters*, 43, 3746–3753. https://doi.org/10.1002/2016GL068533
- Van Heukelem, L., & Hooker, S. B. (2011). The importance of a quality assurance plan for method validation and minimizing uncertainties in the HPLC analysis of phytoplankton pigments. In S. Roy, C. A. Llewellyn, E. S. Egeland, & G. Johnsen (Eds.), *Phytoplankton pigments: Characterization, chemotaxonomy, and applications in oceanography* (pp. 195–242). Cambridge, UK: Cambridge University Press.
- Van Heukelem, L., & Thomas, C. S. (2001). Computer-assisted high-performance liquid chromatography method development with applications to the isolation and analysis of phytoplankton pigments. *Journal of Chromatography A*, 910, 31–49. https://doi.org/10.1016/S0378-4347(1000)00603-00604
- van Woesik, R. (2004). Comment on "Coral reef death during the 1997 Indian Ocean dipole linked to Indonesian wildfires". *Science*, 303(5662), 1297–1297. https://doi.org/10.1126/science.1091983.
- Vernet, M., Neori, A., & Haxo, F. T. (1989). Spectral properties and photosynthetic action in red-tide populations of *Prorocentrum micans* and *Gonyaulax polyedra*. *Marine Biology*, 103, 365–371. https://doi.org/10.1007/BF00397271
- Westberry, T. K., Shi, Y. R., Yu, H., Behrenfeld, M. J., & Remer, L. A. (2019). Satellite-detected ocean ecosystem response to volcanic eruptions in the subarctic Northeast Pacific Ocean. Geophysical Research Letters, 46, 11270–11280. https://doi.org/10.1029/2019GL083977
- Westerling, A. L., Hidalgo, H. G., Cayan, D. R., & Swetnam, T. W. (2006). Warming and earlier spring increase Western U.S. forest wildfire activity. *Science*, 313(5789), 940–943. https://doi.org/10.1126/science.1128834
- Wilson, S. T., Hawco, N. J., Armbrust, E. V., Barone, B., Björkman, K. M., Boysen, A. K., et al. (2019). Kīlauea lava fuels phytoplankton bloom in the North Pacific Ocean. *Science*, 365(6457), 1040–1044. https://doi.org/10.1126/science.aax4767.

KRAMER ET AL. 16 of 16