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Phytoplankton assemblage structure in and around a massive under-ice bloom in the Chukchi Sea

Samuel R. Laney*, Heidi M. Sosik

Biology Department, Woods Hole Oceanographic Institution, Woods Hole, MA 02543, USA

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ABSTRACT

Standard and imaging flow cytometry were used to examine the composition of phytoplankton assemblages in and around a massive under-ice bloom in the Chukchi Sea in 2011. In the core of this bloom, roughly 100 km northwest of Hanna Shoal, diatoms represented roughly 87% of the water column carbon-specific biomass of phytoplankton, while nanophytoplankton contributed ~9%. Picoeukaryotes were also observed in this bloom, as were phycoerythrin-containing cells consistent with *Synechococcus* spp., but picophytoplankton, dinoflagellates, and prymnesiophytes each represented only ~1% of the bloom's phytoplankton biomass. More broadly along this part of the Chukchi shelf, nanophytoplankton typically comprised a larger fraction of phytoplankton biomass in the water column, 22% on average but up to 82% at certain locations. Dinoflagellates and prymnesiophytes contributed at most 2% of water column biomass at any location and were most abundant in the deeper slope stations northeast of Hanna Shoal, east of the bloom. Picophytoplankton were most abundant in these deeper slope stations as well, and also in recently ice-free areas to the south around Hanna Shoal. These cell-derived estimates of phytoplankton carbon biomass, which were computed from imaging and standard cytometric observations of phytoplankton cell sizes and from published carbon:volume relationships, agree well with independent measurements of particulate organic carbon concentration from traditional biochemical assays.

1. Introduction

Several large-scale field programs have been conducted in the Chukchi Sea over the past decade, motivated in large part by an interest in understanding better the effects that changing climate will have on Arctic marine ecosystems (Bluhm et al., 2010; Grebmeier and Harvey, 2005; Grebmeier et al., 2009). These field programs have generated considerable new insight into the distribution and seasonality of phytoplankton assemblages in this region of the Arctic Ocean (e.g., Hill et al., 2005; Joo et al., 2012; Min Joo et al., 2012; Sukhanova et al., 2009), but our understanding of phytoplankton assemblages in the Chukchi Sea still contains significant gaps. A notable example is the very high phytoplankton biomass levels that were observed under consolidated pack ice northwest of Hanna Shoal during the ICESCAPE field program (Impacts of Climate on EcoSystems and Chemistry of the Arctic Pacific Environment) in July 2011 (Arrigo et al., 2012). High phytoplankton biomass in ice-covered waters has been documented previously in the Arctic: both directly from measurements of chlorophyll and/or production (Fortier et al., 2002; Mundy et al., 2009; Sherr et al., 2003; Strass and Nothig, 1996) and also indirectly from observed depletion of water column nutrients early in the growing season (e.g., Cota et al., 1996). The 2011 Chukchi event we studied was exceptional in terms of the magnitude of water column biomass, which exceeded 32 g C m^{-2} in the core of this bloom (Arrigo et al., this issue). Its coincidence with drawdown of nitrate in the upper water column and with very high photosynthetic rates and efficiencies signify an active bloom. The surface melt ponds that were observed over the bloom region likely played a role in creating the high level of production, by increasing the coupling of incident sunlight into the water column below (Christensen and Melling, 2010; Perovich et al., 1998). Optical characteristics of melt ponds previously observed in this region of the Arctic (Frey et al., 2011) appear appropriate for providing the light intensities necessary to form an under-ice bloom of this magnitude.

Initial taxonomic assessments of this under-ice bloom focused on the question of its genesis, i.e., whether the bloom arose from phytoplankton living in situ in the water column or if instead it

* Correspondence to: Biology Department, Woods Hole Oceanographic Institution, MS#34 Redfield 1-36, Woods Hole, MA 02543, USA. Tel.: +1 508 289 3647; fax: +1 508 457 2134.
E-mail address: slaney@whoi.edu (S.R. Laney).

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was seeded by algae living in the overlying sea ice. Images of individual nanophytoplankton (2–20 μm) and microphytoplankton (>20 μm), collected with an Imaging FlowCytobot (IFCB, Olson and Sosik, 2007), revealed that the water column assemblages in the immediate core of the bloom were dominated by diatoms of the genera *Chaetoceros*, *Thalassiosira*, and *Fragilariopsis*, taxonomically distinct from the assemblages found in samples taken from cores in the overlying ice (Arrigo et al., 2012). This preliminary assessment of the region around the core of the bloom examined only a subset of the over 50,000 algal images collected in this region during the 2011 ICESCAPE field season. Moreover, standard flow cytometric (FCM) analyses of cells too small to identify from IFCB images indicate that the smaller size fractions may have played a larger role than initially assumed. This broader dataset suggests a much greater degree of complexity in phytoplankton assemblages in this region of the Chukchi Sea than would be inferred from the core of the bloom alone. Here we synthesize these two complementary methods (standard and imaging flow cytometry) to examine in more detail the distribution and taxonomic structure of phytoplankton assemblages in and around this under-ice bloom, as well as the relative contribution of different taxa and size classes to total algal biomass.

2. Methods

2.1. Stations and sampling

This analysis considers 35 stations occupied in the Chukchi Sea in July 2011, along three hydrographic sections extending from recently ice-free waters near Hanna Shoal northward into the ice pack (Fig. 1, Table 1). These stations and transects cover the immediate area of the under-ice bloom reported by Arrigo et al. (2012) northwest of Hanna Shoal, as well as adjoining areas outside the bloom to the east. At each station water samples were collected typically from six depths, beginning at around 1.5 m and including the deep chlorophyll maximum if one was observed. A core suite of measurements was performed on these samples including chlorophyll concentration, particulate organic carbon concentration, and macronutrient concentrations. Materials and methods for these measurements are documented in Arrigo et al. (this issue).

2.2. Standard flow cytometry

A portable flow cytometer (Accuri C6, Becton–Dickson) was used during this field study to determine the abundance of picophytoplankton (<2 μm) and nanophytoplankton (2–20 μm). Seawater samples were prepared by prefiltering through Nitex screening of nominal mesh size 200 μm to remove larger cells, chains, and colonies that might clog the instrument's flow cell. For each sample approximately 200 μl of seawater was counted. Distilled water blanks were measured after each set of samples at every station, and standard beads (PeakFlow P14827, 2.5 μm, 515 nm emission) were also run periodically during the cruise to track instrument behavior, to determine the instrument's level of sensitivity in detecting cells or other particles, and to provide reference data for normalizing the phytoplankton cell scattering measurements into bead units.

Custom software was used to interpret the measured cell scattering and fluorescence data and determine the abundances of pico- and nanoeukaryotes in these samples. Phytoplankton cells were discriminated from other particles by their relative combinations of chlorophyll fluorescence and side scattering. Phycoerythrin fluorescence served as an additional discriminant for identifying very small (ca. 1 μm) particles consistent with cells of *Synechococcus* spp.

In order to assess the relationship between forward scattering and cell size, a laboratory size calibration study was performed with twelve phytoplankton cultures with cell sizes between 1 and ~14 μm. These cultures included two coccolithophores (*Emiliania huxleyi*, *Syracosphaera elongata*), one other prymnesiophyte (*Isochyrsis* sp.), a cyanobacterium (*Synechococcus* sp.), a diatom (*Cylindrotheca fusiformis*), two dinoflagellates (*Amphidinium carterae, Gymnodinium galatheanum*), two chlorophytes (*Dunaliella tertiolecta* and *Nannochloris* sp.), a pelagophyte (*Pelagomonas* sp.), a prasinophyte (*Micromonas pusilla*), and an unidentified small (2.2 μm diameter) eukaryote. Mode cell volume for each culture was estimated by analysis on a Coulter Multisizer II outfitted with a 30 μm orifice and calibrated with NIST traceable 10 μm latex beads (Coulter size standard L10). The mode values of integrated forward light scattering (FSC-A, measured on the same cultures with the Accuri C6 flow cytometer) were normalized to the same 2.5 μm beads measured during the cruise in order to provide results in bead units. A second-order polynomial was fit to these log transformed data, generating an empirical calibration for converting field measurements of Accuri FSC-A into estimates of individual cell volume (Fig. 2). While the fit represents variation across a range of cell sizes and types, cell volume of *Cylindrotheca fusiformis* is underestimated by this approach, which is consistent with previous work showing that relatively low forward light scattering is expected due to the elongated shape of many pennate diatoms (Olson et al., 1989).

This laboratory-derived relationship between Accuri C6 forward scattering and cell size suggests that this flow cytometer does not have the sensitivity necessary to resolve scattering of very small cells (size ~1 μm), because when measured with the Accuri C6 the *Synechococcus* sp. cells had FSC-A values indistinguishable from noise levels. Thus, this data point can be considered an estimate of the detection level intercept for Accuri C6 observations. Since *Synechococcus* is also difficult to size accurately with a Multisizer configured with a 30 μm aperture, its volume was approximated as a 1 μm diameter sphere, as were all cells in the FCM field measurements that were identified as *Synechococcus* by virtue of their phycoerythrin fluorescence. It is important to emphasize that the lack of sufficient light scattering sensitivity to characterize *Synechococcus* does not impact the ability to detect and enumerate these cells with the Accuri C6, because their phycoerythrin and chlorophyll fluorescence signals are readily distinguishable from background.

2.3. Imaging flow cytometry

Digital micrographs of phytoplankton in the nano- and microsize fraction were collected with a variant of the Imaging FlowCytobot based on the design described by Olson and Sosik (2007). Briefly, volumes of seawater (typically 5 ml) were injected through an 860 × 180 μm flow cell through which a 635 nm laser beam was focused. Chlorophyll-containing particles that passed through this beam emitted a fluorescence signal (>650 nm) that was detected by a photomultiplier tube. Fluorescence events triggered a digital camera that captured a micrograph of that particular cell, chain, or colony. A Nitex screen with nominal mesh size of 130 μm was placed on the instrument's sample intake during the ICESCAPE study to prevent larger particles from clogging the flow cell. This screen, combined with the camera field of view, set the effective upper size limit of cells, chains, or colonies seen in these images to those of length ca. 300 μm or less. The lower size limit of cells seen in these IFCB images is a function of the minimum fluorescence intensity needed to trigger the camera. For samples collected during the ICESCAPE study, cells typically above 8 μm

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