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Massive Phytoplankton Blooms Under Arctic Sea Ice

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The seasonal sea ice and snow cover in the Arctic Ocean strongly reflect and attenuate incoming solar radiation. Consequently, current estimates of pan-Arctic primary productivity assume that the growth and biomass of phytoplankton, free-floating single-celled photosynthetic organisms at the base of the marine food web, are negligible in waters beneath ice because of insufficient light (*1*). However, during the 2011 ICESCAPE (Impacts of Climate on EcoSystems and Chemistry of the Arctic Pacific Environment) cruise, we observed a massive phytoplankton bloom that had developed beneath the 0.8- to 1.3-m-thick first-year sea ice on the Chukchi Sea continental shelf.

From 4 to 8 July, we sampled (*2*) along two 250-km transects extending from open water far into the ice pack (fig. S1). Depth-integrated phytoplankton biomass beneath the ice was extremely high (Fig. 1, A and B), about fourfold greater than in open water. This massive under-ice bloom extended for >100 km into the ice pack. Peak particulate organic carbon biomass (28.7 to 32.5 g C m^{-2}) was located far within the pack in the vicinity of the shelf break where ice was thickest and nutrient upwelling had been driven by easterly winds. Biomass was greatest (>1000 mg C m^{-3}) near the ice/seawater interface and was associated with nutrient depletion to depths of 20 to 30 m (Fig. 1, C and D), indicative of phytoplankton, rather than ice algal, growth. Species composition of the bloom was distinct from that in the overlying ice and was overwhelmingly (>80% by cell cross-sectional area) dominated by healthy pelagic diatoms of the genera *Chaetoceros*, *Thalassiosira*, and *Fragilariopsis*. Furthermore, rates of phytoplankton growth (0.83 to 1.44 day^{-1}) and carbon fixation (1.2 to 2.0 mg C mg^{-1} chlorophyll *a* $hour^{-1}$), and the maximum efficiency of photosystem II (>0.5), were high to depths of >50 m within the under-ice bloom.

In contrast, phytoplankton biomass in open waters was markedly lower than that beneath the ice and was greatest at depths of 20 to 50 m (Fig. 1, A and B) because of nutrient depletion near the surface (Fig. 1, C and D). The high oxygen (480 μmol l^{-1}) and low dissolved inorganic carbon (2020 μmol l^{-1}) relative to the low phytoplankton concentrations (~150 mg C m^{-3}) in these nutrient-depleted waters suggest that they had recently supported high rates of phytoplankton growth. Thus, the ice-free portions of both transects likely harbored remnant under-ice blooms that had developed near the surface weeks earlier, when the region was ice-covered.

The light required by the under-ice bloom had to penetrate the fully consolidated ice pack to reach the upper ocean. Light transmission through ice was enhanced by a recent increase in the fraction of first-year ice, which is much thinner (0.5 to 1.8 m) than the historically dominant multiyear ice pack (2 to 4 m), and especially by a high surface melt pond fraction (25 to 50%). Optical measurements showed that the ice beneath these melt ponds transmitted fourfold more incident light (47 to 59%) than adjacent snow-free ice (13 to 18%). Although the under-ice light field was less intense than in ice-free waters, it was sufficient to support the blooms of under-ice phytoplankton, which grew twice as fast at low light as their open ocean counterparts.

The Arctic Ocean has an enormous, mostly ice-covered continental shelf, ~50% of which has surface nitrate concentrations >10 μmol l^{-1} in early spring (*3*), making these potential sites for under-ice phytoplankton blooms. Previous reports hinted at similar blooms in the Barents Sea, Beaufort Sea, and Canadian Arctic Archipelago (*4*–*6*), suggesting that under-ice blooms are widespread. If so, current rates of annual net primary production on Arctic continental shelves, based only on open water measurements, may be drastic underestimates, being 10-fold too low in our study area. Work is still required to determine the timing and spatial distribution of under-ice phytoplankton blooms across the Arctic Ocean, the extent to which they are controlled by thinning sea ice and proliferating melt pond fractions, and how they affect marine ecosystems. This is particularly important if we are to understand and predict the biological and biogeochemical impacts of ongoing and future changes in the Arctic Ocean physical environment.

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Supplementary Materials
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Materials and Methods
Fig. S1
References (*7*–*15*)

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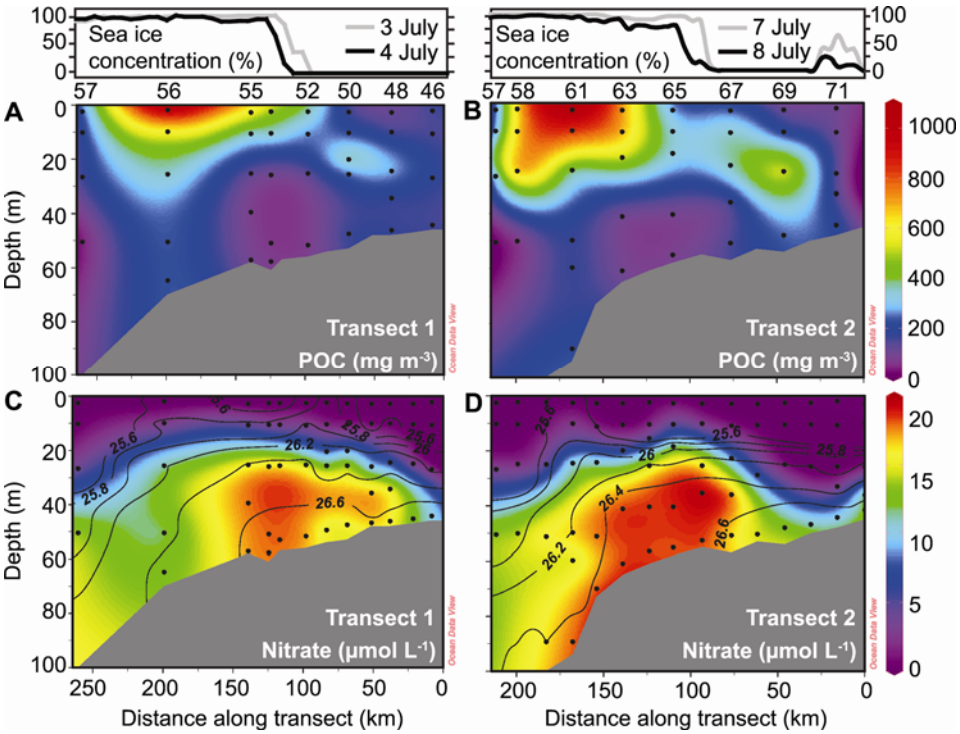

Fig. 1. Under-ice phytoplankton bloom observed during ICESCAPE 2011. (**A**) Particulate organic carbon (POC) and (**C**) nitrate from transect 1. (**B**) POC and (**D**) nitrate from transect 2. Sea ice concentrations and station numbers are shown above (A) and (B); black dots represent sampling depths; black lines denote potential density.

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Supplementary Materials for

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Materials and Methods

Samples for fluorometric analysis of Chl *a* were filtered onto 25 mm Whatman GF/F filters (nominal pore size 0.7 µm) placed in 5 mL of 90% acetone, and extracted in the dark at 3ºC for 24 hrs. Chl *a* was measured fluorometrically (*8*) using a Turner Fluorometer 10-AU (Turner Designs, Inc.).

Particulate organic carbon samples were collected by filtering sub-samples onto pre-combusted (450°C for 4 hrs) 25 mm Whatman GF/F filters. The filters were immediately dried at 60°C and stored dry until analysis. Prior to analysis, the samples were fumed with concentrated HCl, dried at 60°C, and packed into tin capsules (Costech Analytical Technologies, Inc.) for elemental analysis on a Carlo-Erba NA-1500 elemental analyzer. Peach leaves and glutamic acid were used as a calibration standard.

The maximum efficiency of photosystem II (Fv:Fm) was determined by fast repetition rate fluorometry (FRRf) (*9*) on samples collected with Niskin bottles. Samples were dark acclimated for ~30 min at in situ temperatures before measurement with the FRRf. Blanks for individual samples analyzed by FRRf were prepared by gentle filtration through a 0.2 µm polycarbonate syringe filter before measurement using identical protocols. All Fv:Fm values were corrected for blank effects (*10*).

Photosynthesis versus irradiance relationships (P^*_m, α^*, E_k) were determined using a modified ^{14}C-bicarbonate incorporation technique (*11-12*). Carbon uptake, normalized by Chl *a* concentration, was calculated from radioisotope incorporation, and the data were fit by least squares nonlinear regression (*13*). P-E parameters were used with under-ice light profiles to estimate rates of depth-integrated daily gross primary production. Specific growth rate (μ, d^{-1}) in surface waters was calculated by multiplying the photosynthetic rate (P*) by the POC:Chl *a* ratio.

Water samples collected from Niskin bottles were analyzed for nitrate (NO_3) and nitrite (NO_2) concentrations with a Seal Analytical continuous-flow AutoAnalyzer 3 (AA3) using a modification of the Armstrong *et al.* (*14*) procedure. For the NO_3 analysis, seawater samples were passed through a cadmium reduction column where NO_3 was quantitatively reduced to NO_2. Sulfanilamide was then introduced to the sample stream followed by N-(1-naphthyl) ethylenediamine dihydrochloride which couples to form a red azo dye. The stream was then passed through a flow cell and the absorbance measured at 520 nm. The same technique was employed for NO_2 analysis,

except the cadmium column was bypassed. Absorbance vs. concentration standard curves were used to determine the molar concentration of the combined [NO_3+NO_2] and NO_2 alone.

Seawater samples for DIC were drawn from the Niskin samplers into pre-cleaned ~300 mL borosilicate bottles, poisoned with $HgCl_2$ to halt biological activity, sealed, and returned to the Bermuda Institute of Ocean Sciences (BIOS) for analysis. DIC samples were analyzed using a highly precise (~0.025%; <0.5 mmoles kg^{-1}) gas extraction/coulometric detection system (*15*). Analyses of Certified Reference Materials (provided by A. G. Dickson, Scripps Institution of Oceanography) ensured that the accuracy of the DIC and TA measurements was 0.05% (~0.5 mmoles kg^{-1}) and 0.1% (~2 mmoles kg^{-1}), respectively.

Phytoplankton assemblage composition was examined using imaging-in-flow cytometry, where high-speed photomicrographs of individual cells and chains were identified to the genus level or better using automated classification (*16*) followed by manual verification.

Fig. S1. MODIS-Aqua satellite image of the northern Chukchi Sea showing the distribution of sea ice on 8 July 2011 and the location of stations sampled during the ICESCAPE 2011 cruise. Black indicates open water. Lines show the position of the ice edge on the indicated dates (AMSR-E). Stations 46-57 are part of Transect 1 and stations 57-71 are Transect 2.

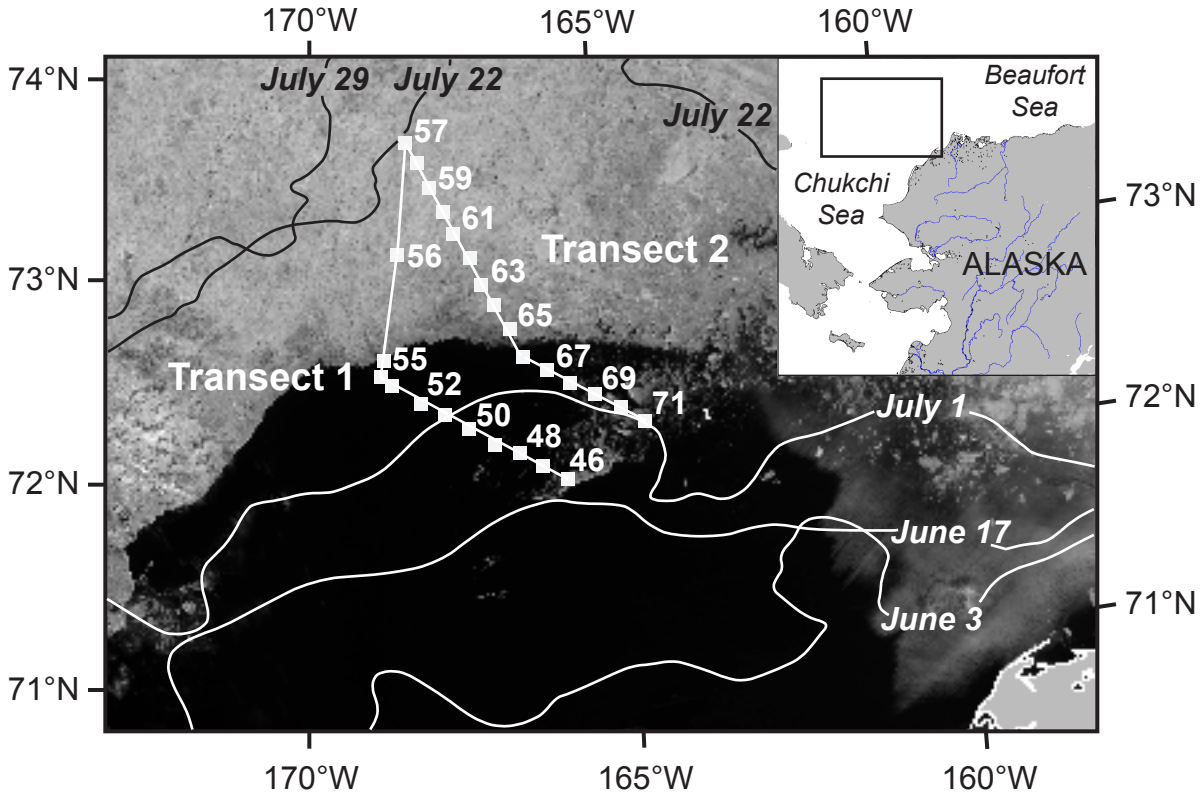
170°W
165°W
160°W
74°N
73°N
72°N
71°N
July 29
July 22
July 22
57
59
61
56
63
65
67
69
71
Transect 2
Transect 1
55
52
50
48
46
July 1
June 17
June 3
Beaufort Sea
Chukchi Sea
ALASKA

Fig. S1

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