Smallest Algae Thrive As the Arctic Ocean Freshens

William K. W. Li,[1]* Fiona A. McLaughlin,[2] Connie Lovejoy,[3] Eddy C. Carmack[2]

As global climate changes, conditions will favor some organisms more than others; there will be ecological winners and losers. In the Arctic, rising air temperature, increasing precipitation, higher river flows, and declining snow cover have lead to large and rapid change in the upper ocean. Surface waters in the Canada Basin have also freshened in recent years because of increased sea ice meltwater and episodic input of large river runoff (*1*). The reduction of sea ice in summer, which is occurring more rapidly than forecasted (*2*), may affect phytoplankton production. As the ice edge retreats away from the continental shelf break, wind-driven upwelling of deep nutrient-rich waters can be expected to enhance shelf production (*3*). A greater open sunlit area and a longer growing season also combine to increase annual primary production (*4*); however, Arctic phytoplankton production appears to be limited by the supply of nitrogen and not cumulative irradiance (*5*). The constraints and requirements imposed by nutrients differ among phytoplankton types, so the response to change presumably differs.

Here, we show that, in the changing Arctic Ocean, the smallest phytoplankton cells thrive but larger cells languish. Although the time series of basinwide summer averages is short, the trend of a warmer and fresher upper ocean is evident (Fig. 1A) from a repeated survey of 23 stations (figs. S1 and S2). The density of deep water has remained about the same over this period, so the decreasing density of the upper ocean results in stronger stratification (Fig. 1A). Similarly, deep water nutrients have not changed, but upper ocean nutrients have decreased (Fig. 1A). Picoplankton, being very small (<2 μm diameter), have a large surface-area-to-volume ratio that provides effective acquisition of nutrient solutes and photons, as well as hydrodynamic resistance to sinking. Predictably (*6*), these cells increased (Fig. 1B) in a regime of lower nitrate supply and greater hydrodynamic stability. Conversely, larger nanoplankton (2 to 20 μm) decreased (Fig. 1B). Upper ocean bacterioplankton increased at the same relative rate (~10% year^{-1}) as picophytoplankton, but deep ocean bacterioplankton remain unchanged (Fig. 1C), suggesting that heterotrophic and photosynthetic changes are coupled in the picoplankton. A reduction in community average body size because of an increase in the abundance of individuals belonging to small-sized species may be a common response to global warming (*7*).

Total phytoplankton biomass, represented as the universal photosynthetic pigment chlorophyll *a*, remained unchanged (Fig. 1B). This biomass, alternately represented as the sum of diagnostic pigments (*8*), is largely (~85%) a complementary mix of cells containing either chlorophyll *b* (picoplanktonic green flagellates) or fucoxanthin (microplanktonic diatoms) (Fig. 1D). Prasinophytes, especially a genetically unique pan-Arctic cold-adapted ecotype of *Micromonas*, constitute a large proportion of picophytoplankton in these waters (*9*). Accepting a time-for-space substitution, the observed increase in picoplankton may thus be associated with a redistribution of pigment groups within the community observed across stations. A secular trend cannot be discerned without a much longer observational time series because of inherent interannual variability. However, if current changes persist, an altered food web may be expected because community size structure is a strong determinant of ecosystem carbon flux. Picoplankton-based systems tend not to support large exports of biogenic carbon, either for extraction (e.g., harvest) or for sequestration (e.g., burial).

References and Notes

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Supporting Online Material

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Materials and Methods
Figs. S1 and S2
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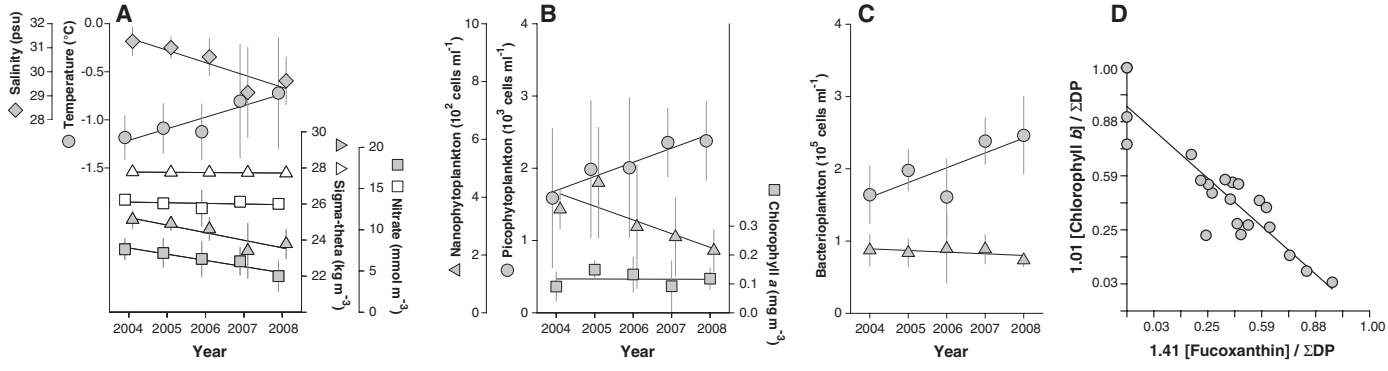

Fig. 1. Summer conditions in the Canada Basin. (**A**) Upper ocean (gray symbols) temperature (P = 0.05), salinity (P = 0.0004), density (P = 0.001), and nitrate (P = 0.06); deep ocean (open symbols) density (P = 0.8) and nitrate (P = 0.9). (**B**) Upper ocean picophytoplankton (P = 0.01), nanophytoplankton (P = 0.09), and chlorophyll *a* (P = 1.0). (**C**) Upper ocean (circles, P = 0.09) and deep ocean (triangles, P = 0.3) bacterioplankton. Error bars are standard deviation of station averages (fig. S1); probability values test for significance of linear regression. (**D**) Proportion (p) of phytoplankton biomass (ΣDP is the sum of diagnostic pigments) represented by green flagellates (1.01Chl*b*) versus diatoms (1.41Fucoxanthin) from 2007 station survey shown on angular transformed scale (arcsin$p^{1/2}$) for normalization of platykurtic distribution, according to pigment scheme of Uitz *et al.* (*8*).

Supporting Online Material for

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Materials and Methods

Hydrographic observations and sampling were carried out in the Canada Basin (Fig. S1) every summer from 2004 to 2008 on the *CCGS Louis S. St-Laurent*. The sampling window was approximately the same in each year (Aug 9-29, 2004; Aug 5-30, 2005; Aug 10-Sep 12, 2006; Jul 31-Aug 27, 2007; Jul 26-Aug 19, 2008). A general description of the cruises appears elsewhere [*S1*]. Seawater samples were collected in Niskin bottles mounted on a CTD rosette and then transferred into smaller bottles for analysis. The collection and analysis of physical (temperature, salinity, density) and chemical (nitrate, silicate, phosphate, chlorophyll *a*) data have been described [*S2*].

Seawater samples for flow cytometric analysis of picophytoplankton, nanophytoplankton and bacterioplankton (*Bacteria* and *Archaea* together) were preserved, stored and analyzed as in our previous studies [*S3*]. Using standard protocols for cytometric identification [*S4*], we determined that phytoplankton in the Canada Basin were almost all eukaryotic algae (>99.5%); in general, phycoerythrin-containing picophytoplankton (presumably cyanobacteria) comprised only 0.5% of detected autofluorescent cells.

Samples for photosynthetic pigment chromatography were collected during the 2007 cruise. Seston from one liter seawater was filtered onto glass fibre membrane (25 mm GF/F), quick frozen in liquid nitrogen, and stored at -80^{o}C. In the laboratory, samples were analyzed by high-performance liquid chromatography using a C_{18} column in combination with a methanol-based, reversed-phase binary gradient system (*S5*].

The horizontal distribution (Fig. S1) and vertical distribution (Fig. S2) of physical, chemical and biological properties were averaged as follows to smooth out spatial variability in order to discern change over time. The depth of 150 m approximates the zone of large vertical transition

in both seawater density and nutrients (Fig. S2). Therefore we combined all measurements at each station above 150 m to give an upper ocean station average, and combined all measurements below 150 m to give a deep ocean station average. An annual average for Canada Basin as a whole was taken by combining all station averages in each year.

Fig. S1 (A) Station map. Depth-averaged upper ocean (z≤150m) properties at 23 individual stations showing average and standard deviation over 5 years: **(B)** Temperature **(C)** Salinity **(D)** Chlorophyll *a* **(E)** Nitrate **(F)** Silicate **(G)** Phosphate **(H)** Picophytoplankton **(I)** Nanophytoplankton **(J**) Bacterioplankton.

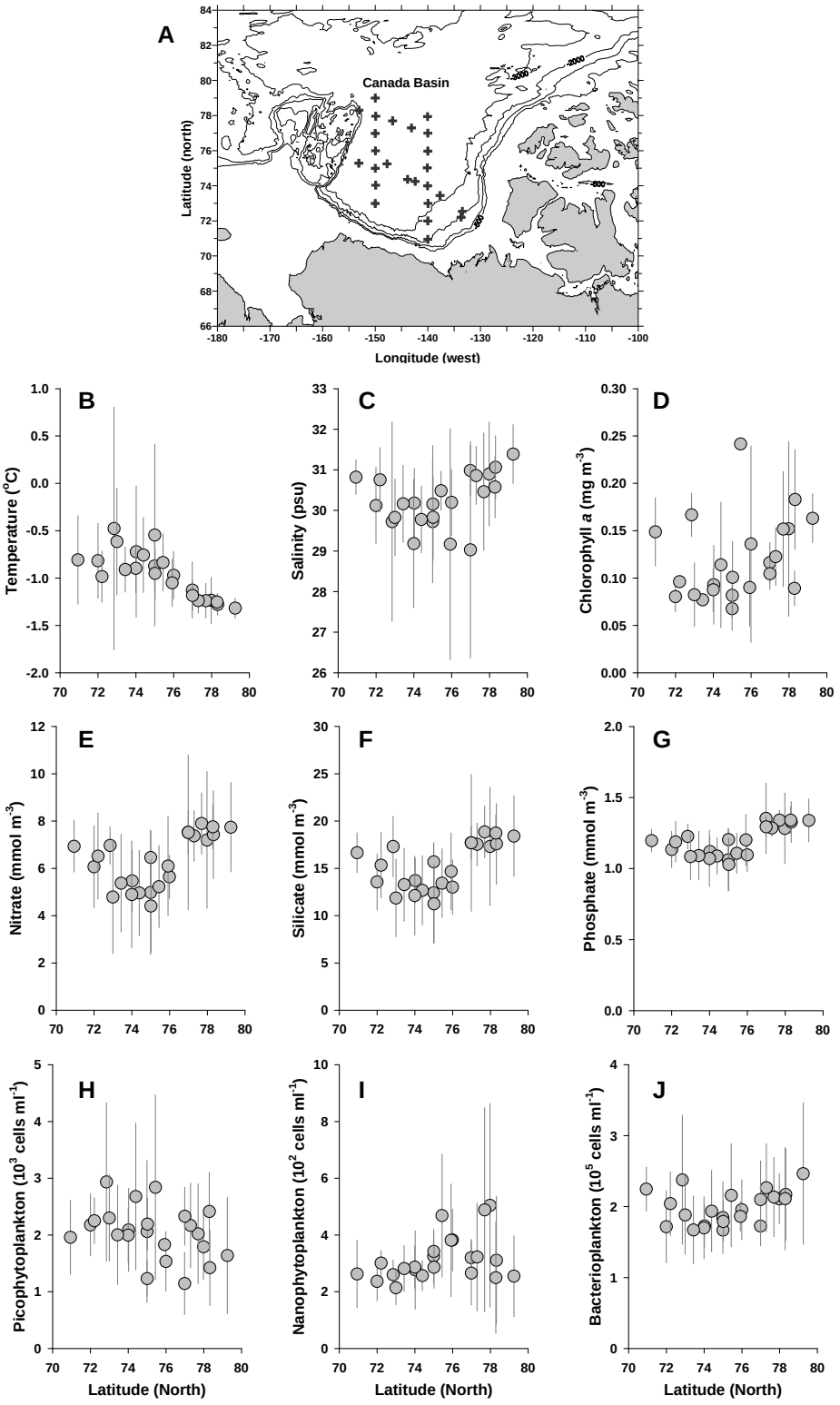
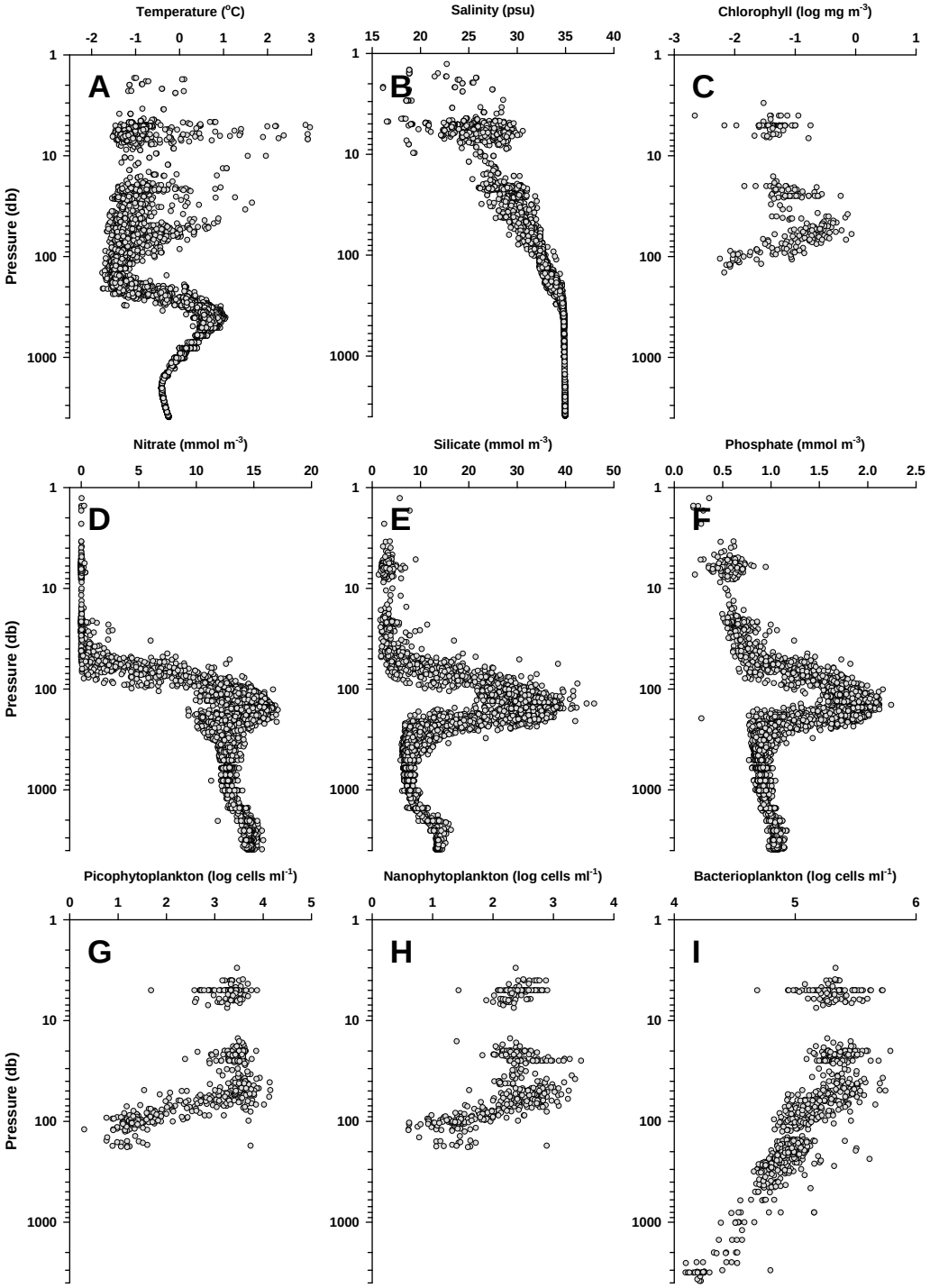


Fig. S2 Composite depth profiles from all stations and all years. **(A)** Temperature **(B)** Salinity **(C)** Chlorophyll *a* **(D)** Nitrate **(E)** Silicate **(F)** Phosphate **(G)** Picophytoplankton **(H)** Nanophytoplankton **(I)** Bacterioplankton.



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