Export of Algal Biomass from the Melting Arctic Sea Ice

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Export of Algal Biomass from the Melting Arctic Sea Ice

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In the Arctic, under-ice primary production is limited to summer months and is not only restricted by ice thickness and snow cover but also by the stratification of the water column, which constrains nutrient supply for algal growth. RV Polarstern visited the ice-covered Eastern Central basins between 82-89°N and 30-130°E in summer 2012 when Arctic sea ice declined to a record minimum. During this cruise, we observed a widespread deposition of ice algal biomass of on average 9 g C per m^2 to the deep-sea floor of the Central Arctic basins. Data from this cruise will contribute to assessing the impact of current climate change on Arctic productivity, biodiversity, and ecological function.

Primary productivity in the Central Arctic is limited by light and nutrients. Photosynthetically active radiation (PAR) for under-ice primary production is only available from May to August but is locally restricted by ice thickness and snow cover (*1–4*). Owing to stratification (*5*, *6*), the mixed layer depth is limited to 10-30 m in summer (Table 1), which constrains the nutrient supply for algal growth (*7*). Hence, average estimates for primary production (PP) in the ice-covered Central Arctic are low, of the order of 1-25 g C m^{-2} yr^{-1} (*8*, *9*). The contribution of ice algae is not well constrained ranging from 0-80% (*10–13*). However, as a consequence of Arctic warming, sub-ice primary productivity may be boosted by higher light transmission through thinning sea ice (*3*, *14*, *15*), and the increase in melt pond coverage during summer (*4*, *16*).

Assessing the consequences of current climate change in the Central Arctic regions remains difficult, because reliable baselines for Arctic productivity, biodiversity, and ecological function are lacking (reviewed by *17*). During the 2012 sea ice minimum, RV "Polarstern" visited the ice-covered Eastern Central basins between 82-89°N and 30-130°E (Fig. 1). In this area, thick multiyear sea ice has been largely lost as a result of to melt by atmospheric heat (*18*). Our airborne electromagnetic measurements confirmed that first year ice dominated (>95%), with an average modal thickness of less than a meter and a melt pond cover of 30-40%.

Previous investigations of the underside of Arctic sea-ice found that the diatom *Melosira arctica* grows meter-long filaments, anchoring in troughs and depressions under ice floes, and covering up to 40-80% of the underside of undisturbed ice floes (*12*, *19–24*) (Fig. 2). Warming and melting leads to their rapid sedimentation (*20–23*). Deposition of *Melosira* strands had been observed on the seafloor of Arctic shelves (*12*, *21*), but their contribution to carbon export in the ice-covered basins remains unknown (*25*, *26*). Particulate organic carbon flux to the deep sea, measured by seafloor carbon demand (*25*) and by sediment traps moored in the Amundsen Basin (*27*) was around 1 g C m^{-2} yr^{-1} (>1500 m) in the 1990s, with a peak contribution of sub-ice algae of up to 28% in August (*27*). Repeated measurements during the first Arctic-wide sea-ice minimum in 2005-2007 showed an increased carbon flux of 6.5 g C m^{-2} yr^{-1} (850m); peaking in July (*28*).

During the expedition IceArc in summer 2012, we observed in seven out of eight regions seafloor deposits of fresh *Melosira arctica* strands and other sub-ice algae at 3500-4400m water depth (Fig. 1, fig. S1, and movies). Patches of algae of 1-50 cm in diameter covered up to 10% of the seafloor. This attracted opportunistic megafauna, such as the deep-sea holothurians *Kolga hyalina* (*29*), *Elpidia heckeri* and the ophiurid *Ophiostriatus striatus*, which were observed to feed on the *Melosira* strands. Based on their color, chlorophyll *a* content, and chloroplast morphology, the freshest algal deposits were observed at the northernmost stations #7,8 (>87°N). Stations #4-6 (82-85°N) north of the Laptev Sea margin showed degraded algal deposits. In this area, megafauna biomass was substantially elevated, as was the pigment concentration of holothurian gut content (Table 1). The larger body sizes (>6 cm) and apparent fecundity of the *Kolga* population (based on gonad sizes) in this area suggested sources of food had been available for at least 2 months, and that the main algal flux had occurred before June. This matches observations of rapid melt and export of ice from the Laptev Sea as early as May 2012. By July, large open water areas had appeared within the ice zone up to 85°N (Fig. 1), causing a rapid decline of the sea ice cover, reflected in 1-2m of melt water content above the winter thermocline (Table 1).

Our surveys showed shreds of *Melosira arctica* (Table 1), indicating their melt-out earlier in the season (*23*). At 3500-4400 m depth, deposits of coiled *Melosira* strands (diameters of 5-12 cm) covered 0.1-10% of the seafloor. The carbon deposition by sub-ice algae was estimated to be equivalent to 1-156 g C m^{-2} (median 9 g C m^{-2}) (Table 1). For comparison, the 2012 pelagic new production in the same regions was estimated to be 7-16 g C m^{-2} (median 11 g C m^{-2}) (Table 1), with a contribution by diatoms of 36% based on silicate inventories (Table 1). *Melosira* strands are not used as food in the pelagial and sink rapidly to the seafloor (*23*). This results in a contribution of at least 45% of total primary production and >85% of carbon export in 2012.

The algal deposits at the seafloor and extracts of *Kolga* gut at stations #3, 4, 7 and8 contained living *Melosira* cells with green chloroplasts and lipid vesicles (Fig. 2). The algal deposits had variable high concentrations of chloroplast pigment equivalents (CPE, 27 ± 21 µg cm^{-3}; n = 18), and a high chlorophyll *a* to total pigment ratio (51 ± 18%). In comparison, pigment contents of bare sediments next to the patches were low with 0.8 ± 0.3 µg cm^{-3}, matching concentrations found in the 1990s (*25*). The gut contents of *Kolga* specimens showed even higher pigment concentrations of on average 51 ± 47 µg cm^{-3} (Chl*a*/CPE ratio of 41 ± 14%; n = 15), and algae recovered from guts were still photosynthesizing when exposed to light (*30*).

Previous investigations focusing on oligotrophic deep-sea sediments have found a direct relationship between carbon flux, benthic biomass and remineralization rates (*31–35*). However, despite the widespread deposition of algae observed in the Central Eastern basins, apparently only sediment bacteria (as estimated from respiration rates; fig. S2), and large mobile megafauna had profited from the ice-algae deposition. Infauna burrows and tubes were rare, indicating an absence of the sediment-dwelling macrofauna characteristic of other deep-sea basins with seasonally sedimenting phytoplankton blooms (reviewed in *36*). Furthermore, the bare sediments next to the algal deposits maintained oxygen fluxes of only 0.3-0.4 mmol m^{-2} d^{-1}, equivalent to a carbon demand of 1-2 g C m^{-2} yr^{-1}. Such low rates are typical for oligotrophic deep-sea sediments (*37*, *38*) and match carbon export fluxes measured in the 1990s in this area (*25*, *27*). In contrast, in situ and ex situ microprofiling of diffusive oxygen fluxes into sediments covered by algal aggregates showed elevated rates of 5-6 O_2 mmol m^{-2} d^{-1}, equivalent to carbon fluxes of 25 g C m^{-2} yr^{-1} (station#7,8; fig. S2). This suggests significant microbial respiration (13-60%) of the algal carbon input. Accordingly, in cores covered by *Melosira* strands, oxygen penetration in the sediment was reduced to a few mm compared with the surrounding sediment, where oxygen penetrated >50 cm (fig. S1). Hence, if high exports of sea-ice algae had occurred regularly before 2012, oxygen penetration depth would have been less than observed, independent of the fresh *Melosira* deposits (*30*). Hence, we conclude that massive algal falls were rare.

Arctic climate models predict a further decline in the sea ice cover, toward a largely ice-free Arctic in coming decades (*39*). Our observations support the hypothesis (*14*) that the current sea-ice thinning and increasing melt-pond cover may be enhancing under-ice productivity and ice-algae export with ecological consequences from the surface ocean to the deep sea.

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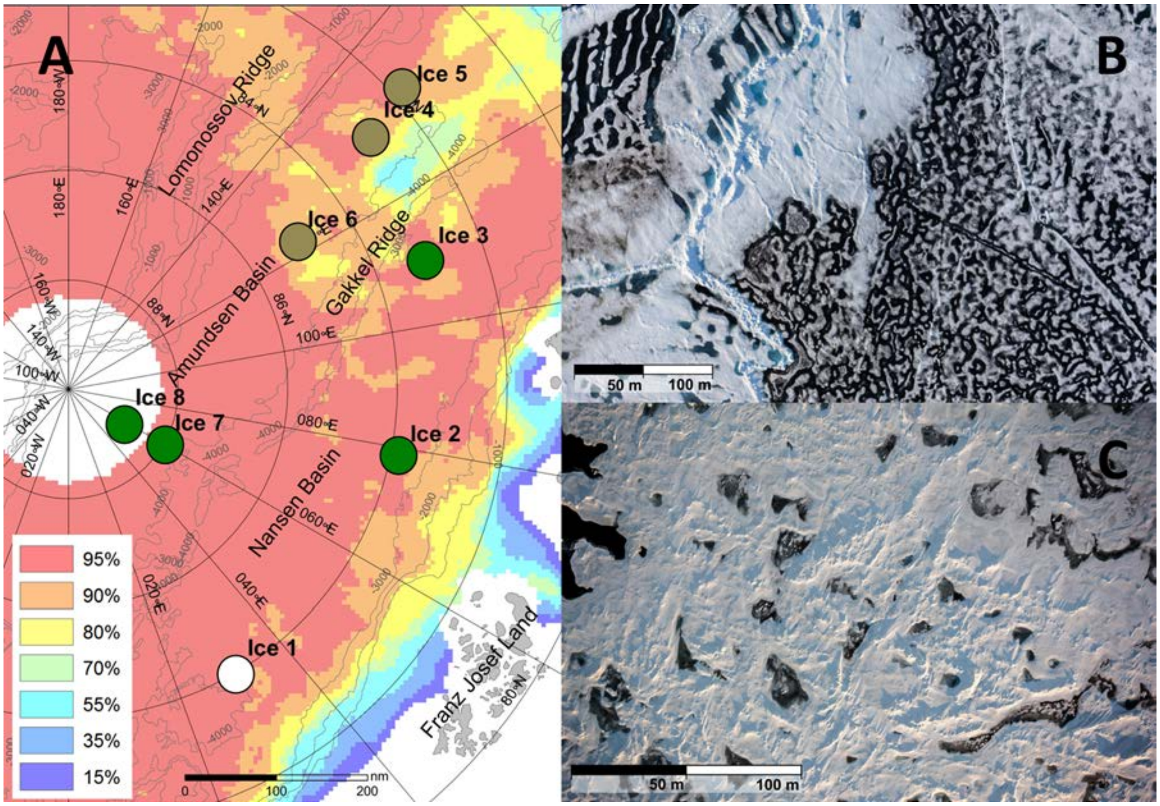

Fig. 1. Ice conditions during RV Polarstern Expedition IceArc (ARK27-3, 02 August to 08 October 2012). (**A**) Left: Ice cover in July 2012 in %. Ice stations with fresh and degraded algal deposits are marked by green and brown circles, respectively. White indicates no deposits. (**B**) Upper right: aerial image of Ice#3 mid August. (**C**) Lower right: aerial image of Ice#6 mid September.

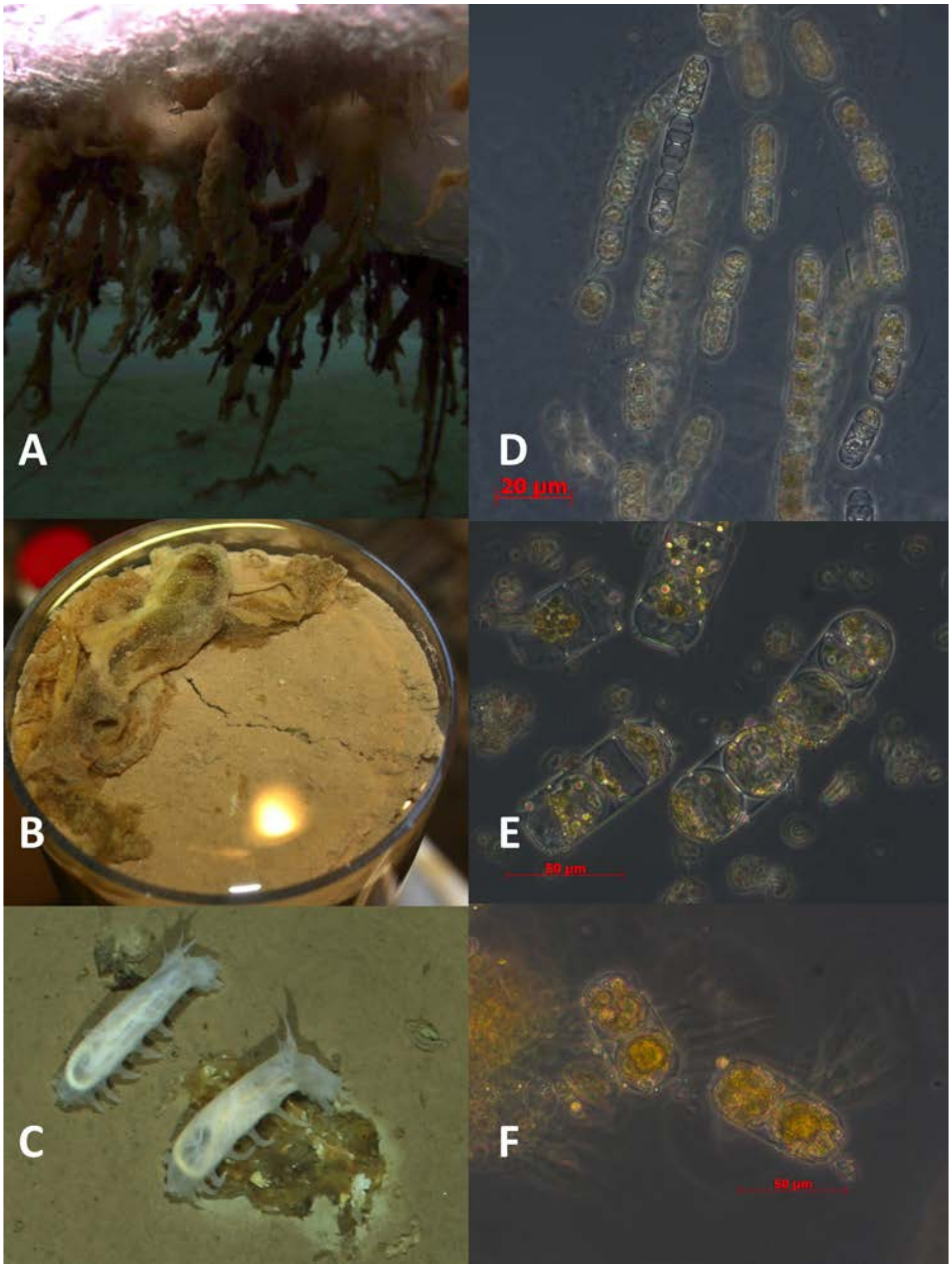

Fig. 2. *Melosira arctica* aggregations. Strands (~20 cm) of Melosira (**A**) under ice (Ice#7); at the seafloor (**B**) (Ice#7), and (**C**) photographed in situ with *Kolga hyalina* grazing on deposits (Ice#3). (**D** to **F**) Microscopic images of *Melosira* cells from (A), (B), and (C) (extract of *Kolga* gut).

Table 1. Distribution of algal aggregates and characteristics of sea ice stations investigated. Methods are provided in the SM. Where available, averages and standard deviations are given.

Ice station (#)	1	2	3	4	5	6	7	8
*Event	PS80_224	PS80_237	PS80_255	PS80_277	PS80_323	PS80_335	PS80_349	PS80_360
Date	8/9/12	8/14/12	8/20/12	8/25/12	9/4/12	9/7/12	9/18/12	9/22/12
Latitude (N)	84°3.03'	83°59.19'	82°40.24'	82°52.95'	81°55.53'	85°06.11'	87°56.01'	88°49.66'
Longitude (E)	031°6.83'	078°6.20'	109°35.37	130°7.77'	131° 7.72'	122°14.72'	61°13.04'	58°51.81'
Sea ice cover (%)	80%	80%	70%	80%	60%	50%	100%	100%
Ice thickness (m)	1.0-1.2	1.2-2.0	0.7-1.2	0.7-0.9	1.2-1.7	0.9-1.7	1.2-1.8	1.1-1.8
First/multi year ice	FYI	FYI	FYI	FYI	FYI	FYI/MYI	FYI/MYI	FYI/MYI
Meltpond cover (%)	40%	20%	40%	50%	10%	30%	20%	20%
Drift (kn)	0.14±0.1	0.35±0.2	0.55±0.2	0.24±0.1	0.26±0.1	0.29±0.2	0.01±0.0	0.17±0.1
†Surf. Radiation (W m^{-2})	150±93	97±59	60±38	56±45	62±76	26±23	11±6	5±3
PAR under ice (W m^{-2})	33	5	9	n.d.	3	2	<1	<<1
Atmospheric temp. (°C)	-1.5	-1.2	0.3	-0.3	-3.3	-1.6	-3.9	-10.1
Seawater temp. (5m, °C)	-1.5	-1.5	-1.6	-1.5	-1.5	-1.5	-1.8	-1.7
Salinity (5m)	33.0	33.2	32.8	31.2	30.6	30.3	33.1	32.9
Mixed layer depth (m)	15	21	16	23	20	20	31	30
‡Melt water (m)	0.5	0.7	0.7	1.1	2.3	2.2	0.8	0.9
Nitrate conc. (µM, ‡0-2m)	2.89	3.08	0.29	0.42	0.1	0.08	0.97	0.49
N:Si/N:P (‡0-2 m)	3/10	2/10	0.3/2	0.1/2	0.03/1	0.02/0.4	0.02/0.3	0.3/2
§^{14}C-PP (mgC m^{-2} d^{-1})	62	9	19	36	39	10	5	4
‡New PP (gC m^{-2} yr^{-1})	16	7	12	7	9	10	16	15
‡Diatom contrib. (%)	40	28	32	24	n.a.	n.a.	41	40
Sub-ice algal cover (%)	0.04	0.19	<0.01	n.d.	0.04	0.03	0.55	0.13
Ice algae composition	‖div. algae	‖div. algae	Melosira	n.d.	Melosira	Melosira	Melosira	Melosira
Seafloor algal cover (%)	0	0.03±0.04	1.3±0.4	¶0.33±0.4	¶0.5±0.2	¶0.8±0.6	2.2±0.7	10.4±0.5
Pigment conc. sed. (µg cm^{-3})	0.7±0.1	1.4±0.3	1.0±0.3	1.0±0.4	0.7±0.2	0.5±0.1	0.6±0.1	0.8±0.5
Chl*a*/CPE ratio (%)	10	17	22	22	18	14	14	14
Megafauna biomass (g wet weight m^{-2})	0.42	1.01	3.36	1.07	3.19	5.49	3.46	0.33
Gut CPE (µg cm^{-3})	n.d.	n.d.	130±20	41±15	30±2	3±1	48±12	n.d.
Gut Chl*a*/CPE ratio (%)	n.d.	n.d.	43	49	66	22	51	n.d.
Ice algae composition sediment/gut	n.d.	n.d.	Melosira	Melosira +div. algae	Melosira +div. algae	Melosira +div. algae	Melosira	Melosira +div. algae
Ice algae C deposition (gC m^{-2})	0	0.5	20	5	7	11	32	156
water depth (m)	4014	3485	3569	4161	4031	4355	4380	4374

*Supplementary data available at http://doi.pangaea.de/10.1594/PANGAEA.803293
†Refers to incoming global radiation at the surface
‡Estimates based on seasonal inventories of the mixed layer depth of the previous freezing season (see SOM).
§Depth integrated rates for the water column euphotic zone (1% PAR under the ice).
||Div. algae included in various ratios *Porosira* sp., *Pleurosigma*, *Nitzschia* sp., *Fragilariopsis* sp., *Entomoneis* sp, *Chaetoceros* sp., *Navicula* sp., *Cylindrotheca* and other chain-forming pennate diatoms, chloroplasts clumps
¶Estimates include discolored patches/degraded algal patches