

Photosynthetic
production in the
Central Arctic

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et al.

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Photosynthetic production in the Central Arctic during the record sea-ice minimum in 2012

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Abstract

The ice-covered Central Arctic Ocean is characterized by low primary productivity due to light and nutrient limitations. The recent reduction in ice cover has the potential to substantially increase phytoplankton primary production, but little is yet known about the fate of the ice-associated primary production and of the nutrient supply with increasing warming. This study presents results from the Central Arctic Ocean collected during summer 2012, when sea-ice reached a minimum extent since the onset of satellite observations. Net primary productivity (NPP) was measured in the water column, sea ice and melt ponds by $^{14}\text{CO}_2$ uptake at different irradiances. Photosynthesis vs. irradiance (PI) curves were established in laboratory experiments and used to upscale measured NPP to the deep Eurasian Basin (north of 78°N) using the irradiance-based Central Arctic Ocean Primary Productivity (CAOPP) model. In addition, new annual production was calculated from the seasonal nutrient drawdown in the mixed layer since last winter. Results show that ice algae can contribute up to 60% to primary production in the Central Arctic at the end of the season. The ice-covered water column has lower NPP rates than open water due to light limitation. As indicated by the nutrient ratios in the euphotic zone, nitrate was limiting primary production in the deep Eurasian Basin close to the Laptev Sea area, while silicate was the main limiting nutrient at the ice margin near the Atlantic inflow. Although sea-ice cover was substantially reduced in 2012, total annual new production in the Eurasian Basin was $17 \pm 7 \text{ Tg C yr}^{-1}$, which is within the range of estimates of previous years. However, when adding the contribution by sub-ice algae, the annual production for the deep Eurasian Basin (north of 78°N) could double previous estimates for that area with a surplus of 16 Tg C yr^{-1} . Our data suggest that sub-ice algae are an important component of the ice-covered Central Arctic productivity. It remains an important question if their contribution to productivity is on the rise with thinning ice, or if it will decline due to overall sea-ice retreat and be replaced by phytoplankton.

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1 Introduction

Estimates of annual primary production (PP) in the ice-covered Central Arctic Basins are among the lowest of all oceans worldwide (Sakshaug et al., 2004). On an annual base, the total incoming irradiance and the depth of the winter mixing are the two main factors that constrain Arctic primary production (Ardyna et al., 2011; Popova et al., 2010). Available irradiance is generally sparse due to the low angle of the sun around the North Pole, and the attenuation effect of sea ice (Sakshaug and Slagstad, 1991). When enough light becomes available for PP between May and September (Arndt and Nicolaus, 2014; Leu et al., 2011), Arctic phototrophs grow in the water column (phytoplankton), in and below sea ice (sea-ice algae), and in melt ponds (melt-pond algae). Light is the main limiting factor for the phytoplankton below thick ice at the beginning of the productive season (Sherr et al., 2003). However, during the summer months the total incoming irradiance increases since daylight is available during 24 h, and sea ice is melting away. North of 78° N latitude, the productive season is shorter (June to September) than in southern Arctic regions, since it is restricted by the amount of light penetrating through the dense sea-ice cover (Leu et al., 2011). Nutrients become limiting as the season advances (Tremblay and Gagnon, 2009), due to strong vertical stratification and reduced wind-driven mixing affected by sea ice (Carmack et al., 2006).

The Central Arctic is divided into two deep basins separated by the Lomonosov Ridge: the Eurasian and the Amerasian basins. These central basins cover 40% of the Arctic Ocean, but due to their inaccessibility, data for both regions are scarce (Matrai et al., 2013). The two central basins differ in the inflow of waters. Low salinity, phosphate rich and nitrate depleted Pacific waters enter the Amerasian Basin through the Bering Strait. Warm, high salinity Atlantic waters with a higher N:P ratio enter the Eurasian Basin through the Fram Strait, but remain submerged under a layer of fresher Arctic surface water for ~5 years before upwelling (Jones et al., 1998). Since most of the studies regarding nutrient limitation in Arctic waters come from the Amerasian

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CTD75M, Trappenkamp, Germany). Fluorescence in the water column was measured with two fluorometers (Turner Cyclops, California, USA) attached to the ship CTD and the ice-CTD, respectively. Fluorescence values were calibrated a posteriori with chlorophyll *a* (chl *a*) concentrations from water samples using high-performance liquid chromatography (HPLC) as described in Tran et al. (2013) and David et al. (2015). chl *a* in the ice and melt ponds was measured using the same HPLC method.

For the nutrient addition experiments, 20 L of seawater were collected at station 3 at the depth of the maximum chl *a* concentration (25 m) using the ships CTD sampler, and a piece of sea ice of 40 cm × 40 cm was cut with an ice saw at station 8 and melted in the dark in 0.2 μm filtered seawater from the same location (Rozanska et al., 2009; Thomas and Dieckmann, 2010).

2.2 In situ net primary production

Net primary production (NPP) was measured using the ¹⁴C uptake method (Steemann Nielsen, 1952) with minor modifications. Melted sea ice, seawater, and melt pond samples were spiked with 0.1 μCi mL⁻¹ of ¹⁴C labelled sodium bicarbonate (Moravek Biochemicals, Brea, USA) and distributed in 10 clear bottles (20 mL each). Subsequently they were incubated for 12 h at -1.3°C under different scalar irradiances (0–420 μmol photons m⁻² s⁻¹) measured with a spherical sensor (Spherical Micro Quantum Sensor US-SQS/L, Heinz Walz, Effeltrich, Germany). At the end of the incubation, samples were filtered onto 0.2 μm nitrocellulose filters and the particulate radioactive carbon uptake was determined by liquid scintillation counting using Filter count scintillation cocktail (Perkin Elmer, Waltham, USA). The carbon uptake values in the dark were subtracted from the carbon uptake values measured in the light incubations.

Dissolved inorganic carbon (DIC) was measured for each sample using the flow injection system (Hall and Aller, 1992). The DIC concentration was taken into account to calculate the amount of labeled bicarbonate incorporated into the cell. Carbon fixation rates were normalized volumetrically and by chl *a*

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year ice (FYI), water under the ice (WUI) and open water (OW). Key parameters for photosynthetic activity were calculated from the measured PI curves during summer 2012, excluding those where the coefficient of determination of the fit (R^2) was smaller than 0.5. Net primary production (NPP) was calculated analogous to Sect. 2.2 for each point in a 10 km polar stereographic grid as a vertical integration with a resolution of 10 cm in the ice and 1 m in the water column. Downwelling solar irradiances at the surface (PAR) were calculated from the European Centre for Medium-Range Weather Forecast (ECMWF) Era Interim re-analyses (Dee et al., 2011). Downwelling transmitted irradiances underneath the sea-ice were calculated using the light parameterization of Arndt and Nicolaus (2014) based on sea ice data from OSI SAF (Andersen et al., 2007). Light extinction in all media was assumed to follow an exponential decay. For water and sea ice we used the same light extinction coefficients as presented above. NPP was calculated as a function of PAR for every depth multiplied with the according chl *a* concentration and integrated over the euphotic zone (1 % incoming PAR). For pixels with a sea-ice concentration > 15 %, the WUI average PI curve was used, while for pixels with < 15 % sea-ice concentration the OW average PI curve was used. Note that the OW average PI curve is based on data obtained close to the Laptev Sea area. For melt ponds, an average depth of 0.4 m was used based on observations during the expedition (Hendricks et al., 2012). Since satellite-based melt pond cover data were not available for summer 2012, a constant melt pond concentration was used for FYI: 26 % and for MYI: 29 % following Arndt and Nicolaus (2014) and Rösel and Kaleschke (2012). These values are similar to the average melt pond coverage observed during our cruise (30 ± 15 %) (Hendricks et al., 2012). Total INPP was calculated as an average of the three compartments “open water”, “water covered by sea ice” and “water covered by sea ice with melt ponds” weighted with the respective areal fraction. To estimate the total range of INPP we ran the CAOPP model three times using the average, the minimum and the maximum photosynthetic parameters.

To investigate differences in NPP in different sectors of the deep Eurasian Basin due to changes in the sea-ice conditions, we ran the model under two different scenarios:

was filtered through a GF/F filter and the pigments were extracted with 90 % acetone during 24 h (Parsons et al., 1984). The fluorescence was then measured with a Turner Fluorometer (Turner, California, USA).

Nutrient concentrations (nitrate, phosphate and silicate) were measured with a standard photometric method using a Technicon TRAACS 800 continuous flow auto analyzer (Technicon Corporation) according to established methods (Boetius et al., 2013). Five different treatments in duplicate were incubated at 75 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$. This irradiance is slightly higher than the average irradiance below the ice at the end of the productive season to avoid light limitation and prevent photoinhibition. The five treatments consisted on a negative control with no nutrient addition (C-), a positive control with the three nutrients added (C+) and three treatments with one nutrient added in each (N+, P+ and Si+). In each treatment, the added nutrient concentration resembled the concentration of that nutrient in deep waters (> 100m) at the same ice station. Biomass (chl *a*, POC and PON) and nutrients were measured in each treatment after 2 days and compared to the initial value. In parallel a sub-set of four samples (20 mL each) from each treatment were spiked with ^{14}C bicarbonate to estimate NPP as described above. Three samples were incubated under light conditions (75 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$) and one in the dark for 24 h. At the end of the experiments the qualitative algal composition from each treatment was studied with a plankton chamber (Hydro-Bios, Altenholz, Germany) and an inverted light microscope with phase contrast optics (Axiovert 40C, Carl Zeiss, Jena, Germany) with integrated camera (AxioCamMRc, Carl Zeiss, Jena, Germany).

2.5 Annual new production

We determined the mixed layer depth during the previous winter from temperature in our summer CTD profiles of the upper Arctic Ocean, following Rudels (1995) and Korhonen et al. (2013). In the temperature profiles during the Arctic Ocean melting season, the winter mixed layer depth is indicated by a temperature minimum above the lower halocline. Any conservative property, such as salinity, observed at the depth

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communities were adapted (I_k) and the light intensity at which photosynthesis is maximal (I_m) were similar to what they received (I) at the time of sampling. In contrast, phytoplankton below the ice and in open waters, generally received less light than what they would need to perform optimally.

3.3 Nutrient addition experiments

For the first nutrient addition experiment, seawater was collected from 25 m depth at ice station 3. It had low nitrate ($1.3 \mu\text{molL}^{-1}$), phosphate ($0.1 \mu\text{molL}^{-1}$) and silicate ($1.2 \mu\text{molL}^{-1}$) concentrations, and a chl *a* concentration of $1.6 \mu\text{gL}^{-1}$. Four days after the addition of $13 \mu\text{molL}^{-1} \text{NO}_3^-$, $0.8 \mu\text{molL}^{-1} \text{PO}_4^{3-}$, and $10 \mu\text{molL}^{-1} \text{SiO}_4^{3-}$, to reach concentrations below the mixed layer, NPP increased in the silica (Si+) treatment and in the positive control with all nutrients (C+) (Fig. 3a). POC, PON and chl *a* only increased significantly when all nutrients were added (Fig. S3a). The increase in NPP corresponded to a carbon yield of $1.3 \text{mgCL}^{-1} \text{d}^{-1}$, matching the POC increase of $1.6 \text{mgCL}^{-1} \text{d}^{-1}$ and the increase in PON ($0.15 \text{mgNL}^{-1} \text{d}^{-1}$). The C : N ratio in the Si+ and C+ treatments increased compared to the other treatments from 10 to 14. Silicate uptake increased significantly in the Si+ and C+ treatments (1.7 and $1.9 \mu\text{molL}^{-1} \text{d}^{-1}$) compared to the control with no nutrient addition ($0.2 \mu\text{molL}^{-1} \text{d}^{-1}$, Fig. 3b). This would correspond to a silicate yield of $0.07 \text{mg Si L}^{-1} \text{d}^{-1}$. The organism responsible for the response was the chain forming diatom *Chaetoceros socialis* (Fig. S4a).

The sea ice sampled at station 8 was depleted in nutrients with very low nitrate ($0.2 \mu\text{molL}^{-1}$), phosphate ($0.1 \mu\text{molL}^{-1}$) and silicate ($1 \mu\text{molL}^{-1}$) concentrations. In this case, the addition of nutrients resulted in measurable nutrient uptake, but neither in an increase in biomass nor in NPP (Figs. 3c and d and S3b). Nitrate yield in the N+ treatment was $0.019 \text{mgNL}^{-1} \text{d}^{-1}$, twice as much as the PON increase ($0.008 \text{mgNL}^{-1} \text{d}^{-1}$), indicating nitrate storage in the cells. The community composition of this sample was formed by typical sea-ice diatoms in a healthy state (with visible chloroplasts): *Nitzschia* sp., *Pseudonitzschia* sp., *Fragilariopsis* sp. and *Entomoneis* sp. (Fig. S4b).

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13 mgCm⁻²d⁻¹; Table S3 and Fig. 4). Melt ponds INPP ranged between 0.01 and 4 mgCm⁻²d⁻¹, and their contribution to total INPP was highly variable (0.05–34 %). They contributed significantly to INPP at stations 3, 7 and 8 (24–34 %). Sea-ice algae contributed significantly (50–62 %) to total INPP at stations 7 and 8, despite their low total INPP rates (1.5 and 0.5 mgCm⁻²d⁻¹ respectively), because the water column production was very low (Fig. 4).

3.5 Annual new primary production

The depth of the temperature minimum associated with haline convection during last winter had a mean of 55 m but ranged from 15 to 93 m depth (Fig. S5b). Stations north of 85° N covered by MYI showed the deepest values. According to the nutrient profiles at the end of the productive season, the total inorganic nitrogen (NO₃⁻ + NO₂⁻) consumption was 119 ± 46 mmolm⁻². Using the Redfield ratio (106 C : 16 N), we estimated the carbon used up for annual new production from nitrogen consumption to be between 0.6 and 17 gCm⁻²yr⁻¹ (Average: 9.4 ± 3.6 gCm⁻²yr⁻¹, Fig. S6). Assuming a productive season of 120 days (Gradinger, 2009), the average NPP rate for the Eurasian Basin was 78 ± 30 mgCm⁻²d⁻¹, which is in the upper range of our in situ measurements in late summer including sea-ice NPP. This value decreases if we increase the length of the productive period. Indeed, due to earlier sea-ice retreat it might be that the productive season in the Central Arctic was longer in 2012. Annual new production is homogeneously distributed through the Eurasian basin. Only the most northern stations show higher annual NPP (13–17 gCm⁻²yr⁻¹), corresponding to a deeper winter haline convection depth (70–80 m) and therefore, a higher nutrient availability and draw-down.

New production based on phosphate drawdown using Redfield gives a similar range (1–16 gCm⁻²yr⁻¹). Using silicate draw-down in the ratio typical for diatoms (7 C : Si) gives an annual carbon uptake range of 0.01–7 gCm⁻²yr⁻¹, meaning that around 10–50 % of the annual carbon uptake based on nitrate was performed by this group of

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phytoplankton (Fig. S6). Sea-ice algae sampled in August–September showed an C : Si ratio average of 9. Using this higher C : Si ratio, and assuming that sea-ice algae are the main consumer of silicate during the growth season, this would yield annual carbon uptake values 20–30 % higher. However, sea-ice algae may have a C : Si ratio closer to Redfield during the growing season when new production occurs.

3.6 Arctic primary production model: CAOPP estimates

Average PI curves and chl *a* profiles were calculated for each environment from summer 2012 measurements and were used to calculate NPP as a function of available PAR for the Eurasian Basin of the Arctic Ocean (78–90° N, 135° E–45° W) using the CAOPP model. We will present here the results calculated with average parameters, but the minimum and maximum values are available in Table 4. The average total INPP for the Eurasian Basin was 54 mgCm⁻²d⁻¹ in August and 34 mgCm⁻²d⁻¹ in September 2012. We observed a decreasing temporal trend in total INPP from August to September, in parallel with a decrease in incoming irradiance (Fig. 5). On average at a basin scale, in late summer/early autumn, sea-ice algae contributed 6 % to total INPP in the Eurasian Basin, while melt ponds were almost negligible (1 %) (Fig. S8). Algal aggregates trapped in melt ponds were not taken into account due to their patchiness and difficulty to upscale their contribution to NPP (Fernández-Méndez et al., 2014). Ice covered waters contributed significantly less (36 %) to total NPP per month than open water (57 %) north of 78° N.

When running the CAOPP model with the sea-ice conditions of September 1982 (mainly > 2m thick MYI), the NPP in the Eurasian Basin was half the NPP in September 2012 (Table S2) assuming that the nutrient concentrations in surface waters were the same in 1982 than in 2012. The fraction of MYI has been reduced the most in the Laptev Sea, where the NPP has increased 53 % according to our model. In a potential scenario in which the Arctic would be completely ice-free in September and nutrients would remain as in 2012, NPP could increase 60 % on average in the Eurasian Basin north of 78° N with the biggest increases occurring in the Barents and

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(AOS expedition, 1994) refers to sub-ice algal communities formed by sub-ice diatoms like *Melosira arctica*. This diatom was also found to comprise much of the total algal biomass during our expedition at station 7, showing an INPP of $13\text{--}40\text{ mg C m}^{-2}\text{ d}^{-1}$, similar to the AOS expedition estimates (Fernández-Méndez et al., 2014), and even more to total export flux. The rapid sea-ice melt in July/August 2012 lead to major sinking of fresh algal biomass to the seafloor of the Arctic basins (Boetius et al., 2013). An estimated NPP of 9 g C m^{-2} by sub-ice algae sedimented during July and August would result in an additional INPP of 16 Tg C , if upscaled to the Eurasian Basin north of 78° N ($1.8 \times 10^{12}\text{ m}^2$). From our nitrate annual drawdown, we calculated a total carbon uptake of $17 \pm 7\text{ Tg C yr}^{-1}$ in the Eurasian Basin north of 78° N . Considering that sub-ice algae drift together with the sea ice and have access to constant nutrient replenishment during their drift, the total new production could be $17 + 16 = 33 \pm 7\text{ Tg C yr}^{-1}$ in the deep basins of the Eurasian Basin. The overall contribution of sea-ice productivity would be 50%. When including sub-ice algal aggregations such as *Melosira arctica* filaments, the average total production of 33 Tg C yr^{-1} in the Central Arctic is higher than previously estimated (22 Tg C yr^{-1} , Codispoti et al., 2013). Therefore, studies that do not include sea-ice productivity and sub-ice algal aggregations may substantially underestimate annual NPP in the Central Basins.

Melt ponds contributed up to 4% to total INPP, which is in the range of previously reported estimates (< 1 to 10%, Arrigo, 2014; Lee et al., 2012). Some melt ponds also contain significant accumulations of algal biomass (Fernández-Méndez et al., 2014), and hence might also become more important for total Arctic PP as their coverage continues to increase (Lee et al., 2011; Rösel and Kaleschke, 2012). Some of the sea-ice algae trapped in melt ponds can rapidly adapt to the changing conditions, as we observed in their high chl *a* normalized maximum photosynthetic rates compared to all other environments. Sea-ice algae are low light adapted (Table 2; Cota, 1985) and show lower photoinhibition in late summer (Michel et al., 1988; Mundy et al., 2011). However, in June–July when they receive 90% of the annual light flux (Arndt and Nicolaus, 2014), they are probably able to adapt to higher light conditions and have

their peak in production. This would have already been exported to the deep sea when we did our sampling in August–September.

An important question concerns the ability of sea-ice algae to deal with nutrient limitations. Inside the sea-ice and in melt ponds, nutrient concentrations integrated over the ice thickness, were significantly lower than in the water column. N : P molar ratios in sea-ice were in general below Redfield (16 : 1) indicating prior production by ice algae limited by nitrate (Maestrini et al., 1986; Smith et al., 1997). Very high N : Si ratios (> 3) at some stations point towards silicate limitation as well. Sea-ice diatoms can store nutrients in their cytoplasm (Kamp et al., 2011; Needoba and Harrison, 2004). Our nutrient addition experiment (Fig. 3d) suggests that sea-ice algal communities can take up nutrients without increasing their biomass. This may be another useful physiological advantage for sea-ice algae in the oligotrophic conditions of the Central Arctic.

4.2 Light and nutrients as limiting factors

Seasonal light availability in the Central Arctic Ocean limits photosynthesis (Leu et al., 2011; Wassmann and Reigstad, 2011). Our in situ measurements and upscaling results using the CAOPP model clearly show the strong effect of sea-ice cover and season on NPP (Figs. 2 and 5). The comparison between ice-free and ice-covered waters of the Eurasian Basin reveals the indirect effect of sea-ice through light attenuation, limiting phytoplankton productivity in ice-covered waters. This is noticeable at the end of the productive season (mid-September), north of 87° N, below MYI, where the euphotic zone is reduced to the upper 7–15 m (Fig. S5a). Hence, years with an extensive ice melt as in 2012 host double as much NPP in the Eurasian Basin as years with normal sea-ice cover such as 1982 (Table S2).

Sea-ice algae are adapted to low light but can profit from increased light availability in thin ice in late summer (I_k range from sea ice and melt ponds 17–290 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$; Table 2). However, lack of snow covering the ice at the beginning of the growth season can also be detrimental for the sea-ice community due to photoinhibition and ice bottom ablation (Juhl and Krembs, 2010; Lund-Hansen

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et al., 2014; Mundy et al., 2011). In our study, evidence for photoinhibition was mainly recorded in August on sea-ice algae trapped at the ice surface of melt ponds where the irradiance was maximal (up to $279 \mu\text{mol photons m}^{-2} \text{s}^{-1}$, Fig. S1, Table 3). However, the highest irradiance fluxes in 2012 occurred in June (Arndt and Nicolaus, 2014) so the potential for photoinhibition was higher in the earlier summer months, especially if no snow was covering the ice. Phytoplankton on the contrary showed almost no photoinhibition under irradiances up to $420 \mu\text{mol photons m}^{-2} \text{s}^{-1}$, allowing them to potentially benefit even more from an increase in irradiance reaching the water column.

Besides constraining the total amount of carbon that can be converted into biomass during the productive season (Codispoti et al., 2013), nutrients also play an important role since they determine algal photoadaptation (Sakshaug and Slagstad, 1991). During our cruise we identified three different nutrient regimes from integrated molar ratios over the euphotic zone at the end of the productive season (Fig. S2, Table 3). Along the ice margin in the Nansen Basin in August, silicate was the most depleted nutrient with N:Si ratios as high as 3 (Fig. S2), which were also reported for the year 1994 by (Gosselin et al., 1997). This may be due to nitrate input from Atlantic waters (Rudels, 2012), but little is known about upward nutrient mixing rates. In the area adjacent to the Laptev Sea, silicate concentrations were higher, probably due to riverine input (Le Fouest et al., 2012), with N:Si ratios below 1 and N:P ratios (1–9) below Redfield (16), indicating nitrate depletion. In late September north of 85°N , all depth integrated nutrient concentrations were low (Table 3). This indicates a general nutrient and light depletion typical of the end of the season (Wheeler et al., 1997), partly due to the reduced euphotic zone (7–15 m).

When calculating the annual new production from nutrient drawdown for the Eurasian Basin in 2012, estimates derived from nitrogen and phosphate yield similar results ($1\text{--}17 \text{gCm}^{-2} \text{yr}^{-1}$), which are in accordance with the latest maximum net community production estimate for this region ($14 \text{gCm}^{-2} \text{yr}^{-1}$, $n = 6$, Codispoti et al., 2013). Estimates derived from silicate, using a C:Si ratio of 7 (Brzezinski, 1985; Harrison et al., 1977), yield annual NPP rates half of the estimates derived from nitrogen or

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phosphate, suggesting that diatom production makes up for about 50% of annual new production, as biogenic silica is the main component of diatom frustules (Martin-Jézéquel et al., 2000). Assuming that sea-ice algae would contribute the most to silicate uptake during the growth season and that they have a higher C : Si ratio as measured at the end of the season, the contribution of diatoms to annual production would increase up to 70%. However, diatoms typically have close to Redfield carbon to nutrient ratios during the growing season when nutrients are available. The observed N : Si ratios (Fig. S2) suggest that nitrate was limiting NPP in the Amundsen Basin (from the Laptev Sea slope to the North Pole), but silicate was limiting NPP in the Nansen Basin (close to the ice margin in the Kara and Barents sectors) of the Eurasian Basin, that is influenced by Atlantic waters. Thus, diatoms are probably limited in the Nansen Basin as soon as the first spring bloom has consumed all the silicate in the mixed layer. Indeed, the increase in NPP and biomass of the diatom *Chaetoceros socialis* in a sample from the water below the ice at the ice margin, after silicate addition, supports this idea (Figs. 3a and b, S3a, and S4a).

Taking into account the export of sub-ice algae earlier in the season 2012 (Average 9 g C m^{-2} , Boetius et al., 2013) and the C : Si molar ratio of diatoms (7), an average of $107 \text{ mmol Si m}^{-2}$ had already been removed from surface waters before August. Since sea-ice algal production starts earlier than phytoplankton productivity (Søreide et al., 2006), sea-ice algae might contribute to nutrient removal in surface waters at the beginning of the season leaving only some nutrients left for the phytoplankton bloom. However, since most of the sea ice in the Central Arctic originates in the shelf areas of the Eurasian Basin and is then transported by the transpolar drift (Pfirman et al., 1997), the sub-ice algae growing attached to the bottom of the ice might have access to the nutrients mixed up on the shelves, upwelled at the shelf-edge or ice-edge earlier in the season and to the surface nutrients of a wider area while they drift with the ice (Carmack et al., 2006; Fernández-Méndez et al., 2014; Syvertsen, 1991). Our nutrient addition experiment performed on a typical ice-algal community, indicates that sea-ice

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As retreating sea-ice leaves behind more open water areas in summer, different Arctic regions are expected to react differently to the increase in irradiance received (Arrigo et al., 2008). To test this, we removed the ice cover in our forcing input data from our CAOPP model and compared the results from September with our 2012 results (Table S2). Based on the changes in light penetrating through the ice and assuming no change in nutrient availability, total INPP for September would increase by 292 % in the Greenland sector, 56 % in the Barents, 38 % in the Laptev and 23 % in the Kara sector (Table S2). However, the loss of ice-attached biomass, such as sub-ice algal aggregates which are not taken into account in these calculations, might counteract the increase in water column PP as sea-ice disappears. The regional variability of changes is due to different sea-ice coverage of the different areas. However, sea-ice retreat will not only affect light transmission, but also water column stratification that might hinder nutrient upwelling (Codispoti et al., 2013). Depending on the future role of winds and sea-ice drift vs. stratification by freshening and warming, nutrient availability in the euphotic zone could change. Most likely, sea-ice algal productivity will increase and shift to earlier periods of the year, and their rapid export from the melting of their habitat in July and August will decrease nutrient availability (Boetius et al., 2013; Lalande et al., 2009). The phytoplankton community will probably shift from diatoms towards small picoplankton, especially in the silicate limited area of the Eurasian Basin (Boetius et al., 2013; Lalande et al., 2009), with potentially detrimental consequences for the Arctic food web.

4.4 Limitations and uncertainties of Arctic NPP estimates

The Central Arctic remains one of the most challenging environments to sample due to its remoteness and the year-round ice cover on top of its deep basins. The majority of Arctic NPP estimates are from seasonally ice-free waters, mainly shelves, sampled during the spring or summer months (Ardyna et al., 2011; Li et al., 2009). Ice-associated NPP has been widely neglected in previous Arctic PP estimates, because it can not be assessed remotely via satellite-borne sensors (Arrigo and van Dijken, 2011),

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and also due to methodological and logistical problems to measure it in the field (Matrai et al., 2013). Two orders of magnitude uncertainties in NPP estimates for the Central Arctic reflect the high spatial and temporal variability characteristic for this environment (Tremblay et al., 2012). Thus, it remains difficult to establish regionally representative baselines in Arctic NPP, to be able to detect significant changes in productivity related to the on-going sea-ice retreat.

This study provides summer in situ NPP data from the under-sampled Eurasian Basin including water column, sea-ice and melt pond that can be used to validate ocean general circulation models predicting changes in Arctic PP (Ferland et al., 2011; Tremblay et al., 2012). Photosynthetic parameters derived from PI curves under realistic conditions are important for modelling primary productivity (Popova et al., 2012; Vancoppenolle et al., 2013). A combination of in situ obtained photosynthetic parameters and a light parameterization for light transmittance of sea-ice (CAOPP model) enabled us to estimate INPP for the entire Eurasian Basin, including ice-covered areas. Although the CAOPP model does not include nutrient information, the PI curves were measured at the end of the season in nutrient limited waters. Hence, using the same parameters to model PP earlier in the season, when more nutrients are available, will underestimate productivity. Photosynthetic parameters vary locally and seasonally (Behrenfeld and Falkowski, 1997). Therefore, the photosynthetic parameters cover a wide range (Table 2) and are not well constrained. This leads to two orders of magnitude difference between the minimum and the maximum NPP calculated with the model. To constrain the results further, more in situ measurements are needed to capture the regional and temporal variability in photosynthetic parameters.

Another limitation of our upscaling using the CAOPP model is that the light parameterization assumes a constant extinction coefficient in the water column and is not spectrally resolved (Manes and Gradinger, 2009; Palmer et al., 2011; Sakshaug and Slagstad, 1991). This could lead to NPP overestimation in open water coastal areas (Alver et al., 2014). A recent INPP estimate for the Arctic Ocean Basin

including the Amerasian Basin where they measured NPP only in ice-free waters ($0.4 \text{ TgC month}^{-1}$ Arrigo et al., 2011; Bélanger et al., 2012) is at the lower end of our estimated range for the water under the ice in the Eurasian Basin in August ($0.2\text{--}6.8 \text{ TgC month}^{-1}$), but suggests that our model can give realistic estimates. Seasonality remains a critical issue in the Central Arctic since there are still no measurements of early spring photosynthetic parameters from communities thriving in and under the ice. Assessing the algal biomass below the ice using Ice Tethered Profiles (ITPs) that drift with the ice during an entire year might be a great step forward to improve our understanding of the annual cycle of primary production in the central basins (Laney et al., 2014).

5 Conclusions

The Central Arctic basins have been generally regarded as low productivity areas. Due to their inaccessibility they have remained largely under-sampled leading to a lack of baseline data to assess current changes. This study provides measurements of primary production during the record sea-ice minimum in the Eurasian Basin in 2012, and new estimates for all environments where phototrophs thrive: sea-ice, melt ponds and water column. Sea-ice algae can contribute up to 60% to the total INPP in the Central Arctic at the end of the productive season. Comparing our results from 2012 with previous estimates of NPP in the Central Arctic, we conclude that an overall change in NPP magnitude would be foremost related to a change in the role of the ice-algal production and export of sub-ice algal aggregates. Melt ponds can contribute up to 34% locally, but at a larger scale their contribution to INPP is $< 4\%$, excluding local aggregations of sea-ice algae. Ice-covered waters sustain lower NPP than open waters in the late summer season, indicating light limitation. However, over the annual productive period, the role of sub-ice algae may be increasing with the overall thinning of sea-ice. Therefore, an increase in irradiance transmitted through the ice will probably lead to an increase in water column NPP in the Central Basins and a shift towards

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earlier sea-ice based NPP. These shifts in the timing and location of ice-algal blooms are likely to impact life cycle strategies and community composition of zooplankton and under-ice fauna, with unknown consequences for the under ice food-web and export fluxes. However, nutrients will still constrain the annual budget of new production both for sea-ice algae and phytoplankton. In the Eurasian Basin, nitrate limits NPP in the Amundsen Basin and silicate limits diatom-based NPP at the ice margin near the Atlantic water inflow (Nansen Basin). Better understanding of the overall development of Arctic productivity will need year-round long-term observations of nutrient supplies and light availability, as well as of mixing processes and grazer populations.

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**Table 2.** Photosynthetic parameters and incoming irradiance of the different environments in the Central Arctic divided in August and September.

Environment (<i>n</i> PI curves)	Photosynthetic parameters						
	P^b	P_m^b	α	β	I_m	I_k	I
	(mg C (mg chl <i>a</i>) ⁻¹ h ⁻¹)		(mg C (mg chl <i>a</i>) ⁻¹ (μmol photons m ⁻² s ⁻¹) ⁻¹ h ⁻¹)		(μmol photons m ⁻² s ⁻¹)		(μmol photons m ⁻² s ⁻¹)
Mean (Min–Max)							
August							
Melt Pond (<i>n</i> = 4)	2036 (65–6670)	2.8 (0.4–8)	0.05 (0.002–0.15)	13.6 (0.08–50)	379 (135–785)	139 (50–290)	145 (102–279)
Sea Ice (<i>n</i> = 7)	105 (0.08–377)	0.3 (0.07–0.7)	0.005 (0.001–0.01)	0.6 (0–2.3)	326 (166–876)	64 (34–98)	53 (24–229)
Water under the ice (<i>n</i> = 4)	300 (0.2–1160)	0.6 (0.2–1.4)	0.01 (0.003–0.02)	1.9 (0–7.3)	331 (158–787)	56 (29–80)	3 (0.7–22)
Open water (<i>n</i> = 2)	1290 (391–2187)	3.5 (2.2–4.7)	0.05 (0.004–0.08)	7.7 (0.2–15)	797 (143–1450)	293 (52–533)	32 (1.3–140)
September							
Melt Pond (<i>n</i> = 4)	1.8 (1.3–2.5)	1.2 (0.4–2.3)	0.03 (0.004–0.07)	0.003 (0.001–0.004)	187 (144–252)	58 (32–290)	29 (13–91)
Sea Ice (<i>n</i> = 6)	0.07 (0.03–99)	0.06 (0.04–0.2)	0.002 (0.001–0.004)	0 (0–0.5)	127 (96–402)	26 (17–64)	4 (1–38)
Water under the ice (<i>n</i> = 4)	0.5 (0.2–0.8)	0.4 (0.2–0.7)	0.02 (0.01–0.02)	0.001 (0–0.002)	319 (102–599)	26 (14–38)	0.7 (0.2–6)
Open water (<i>n</i> = 7)	0.5 (0.4–0.9)	0.5 (0.3–0.9)	0.03 (0.02–0.05)	0 (0–0.001)	85 (59–734)	15 (9–26)	16 (1.3–240)

P^b is the maximum chl *a* normalized carbon fixation rate if there was no photoinhibition; α is the initial slope of the saturation curve; β is the photoinhibition parameter; P_m^b is the carbon fixation rate at maximal irradiance; I_m is the light intensity at which photosynthesis is maximal; I_k is the adaptation parameter or photoacclimation index. I is the average daily irradiance received in each environment from the surface to the bottom of the pond, the ice or the euphotic zone in the water column.

* Open waters in Sep correspond to the Laptev Sea region.

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Table 3. Nutrient inventories and molar ratios in each environment during summer 2012 separated into the three nutrient regimes observed.

	Nutrients		Silicate	N : P mol : mol	N : Si
	Nitrate (mmol m ⁻²)	Phosphate			
Ice margin (6–18 Aug 2012)					
Melt pond (<i>n</i> = 2)	0.1–0.8	0–0.12	0.01–1.6	6.8–85	0.5–9
Sea ice (<i>n</i> = 2)	0.3–0.8	0.03–1.3	0.2–0.5	0.6–11	0.6–4
Sea water (<i>n</i> = 9)	76–157	7–16	27–77	9–11	1.7–2.8
Laptev Sea (20 Aug–10 Sep 2012)					
Melt pond (<i>n</i> = 4)	0.2–0.4	0–0.15	0.1–0.8	2–114	0.4–5
Sea ice (<i>n</i> = 4)	0.2–0.7	0.01–0.06	0.1–0.4	5.2–15	0.6–4
Sea water (<i>n</i> = 17)	8–126	4.5–19	35–220	1.2–8.6	0.1–1
North of 85° N (18–27 Sep 2012)					
Melt pond (<i>n</i> = 2)	0.06–0.2	0.01–0.06	0.1–0.9	1–18.3	0.2–0.5
Sea ice (<i>n</i> = 2)	0.2–1.7	0.04–0.1	0.1–0.2	4.7–17	1–16
Sea water (<i>n</i> = 6)	4–31.0	1.5–3.5	12–23	3–9	0.3–1.7

Nutrient concentrations in mol L⁻¹ are available in PANGAEA (doi in Table S1). Nutrient concentrations were integrated for melt pond depth, sea-ice thickness and water column euphotic zone (1 % incoming PAR).

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Table 4. Integrated net primary production in the Central Arctic at different times and spatial scales. The number of daily measurements is given in Table 2. The contribution by sub-ice algal aggregates is not included in any of the values presented in this table.

	Integrated net primary production (INPP)					
	Daily In situ Mean \pm SD	Aug	Monthly Mean (Min–Max)		Annual 2012 Mean \pm SD	
INPP in the Eurasian Basin	mgCm ⁻² d ⁻¹	mgCm ⁻² d ⁻¹			gCm ⁻² yr ⁻¹	
Total	24 \pm 19	54	(21–180)	34	(21–65)	9.4 \pm 3.6
Sea Ice	2.2 \pm 4.1	5.8	(0.06–42)	2.6	(0.02–20)	
Melt Ponds	0.9 \pm 1.3	0.5	(0.2–1.7)	0.7	(0.06–3)	
Water under the ice	20 \pm 20	31	(4.5–116)	12	(3–50)	
Open water	84 \pm 38	97	(62–115)	56	(43–50)	
	Mean \cdot Area	Sum				Sum
INPP in the Central Arctic (78° N)	TgCd ⁻¹	TgCmonth ⁻¹				TgCyr ⁻¹
Total	0.09 \pm 0.07	5.7	(1.7–24)	3.4	(1.78–8.45)	36
INPP in the Eurasian Basin	TgCd ⁻¹	TgCmonth ⁻¹				TgCyr ⁻¹
Total	0.04 \pm 0.03	3.1	(1.2–10)	1.9	(1.1–3.6)	17.4 \pm 6.7
Sea Ice	0.004 \pm 0.007	0.2	(0.002–1.7)	0.08	(0.0008–0.6)	
FYI	0.004 \pm 0.009	0.05	(0.002–0.4)	0.008	(0.0004–0.06)	
MYI	0.002 \pm 0.001	0.2	(0.0003–1.2)	0.07	(0.0002–0.5)	
Melt Ponds	0.002 \pm 0.002	0.02	(0.007–0.07)	0.02	(0.002–0.09)	
Water under the ice	0.04 \pm 0.04	1.3	(0.2–6.8)	0.4	(0.1–1.6)	
Open water	0.16 \pm 0.071	1.5	(1–1.8)	1.4	(1–1.3)	

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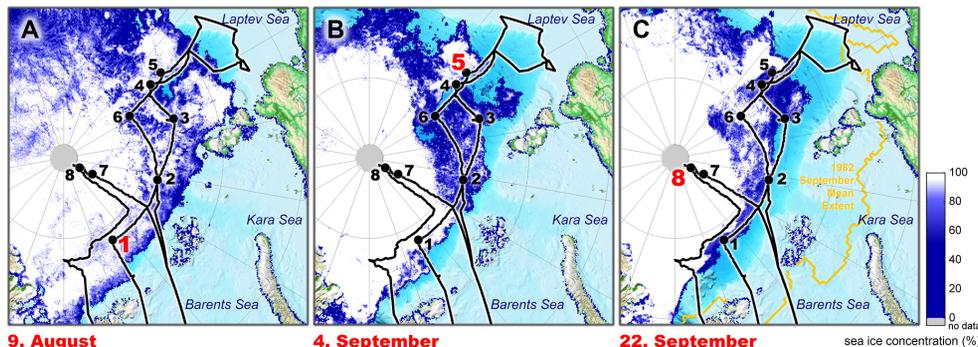


Figure 1. Cruise track and stations sampled in the Eurasian Basin during summer 2012. The different panels show the sea ice concentration at the time of sampling the first ice station in early August (a), the fifth station at the beginning of September (b), and the last ice station in early autumn (c). The sea-ice extent minimum record was reached in early September 2012 and refreezing started two weeks later. For comparison purposes, the mean sea-ice extent for September 1982 is depicted in orange.

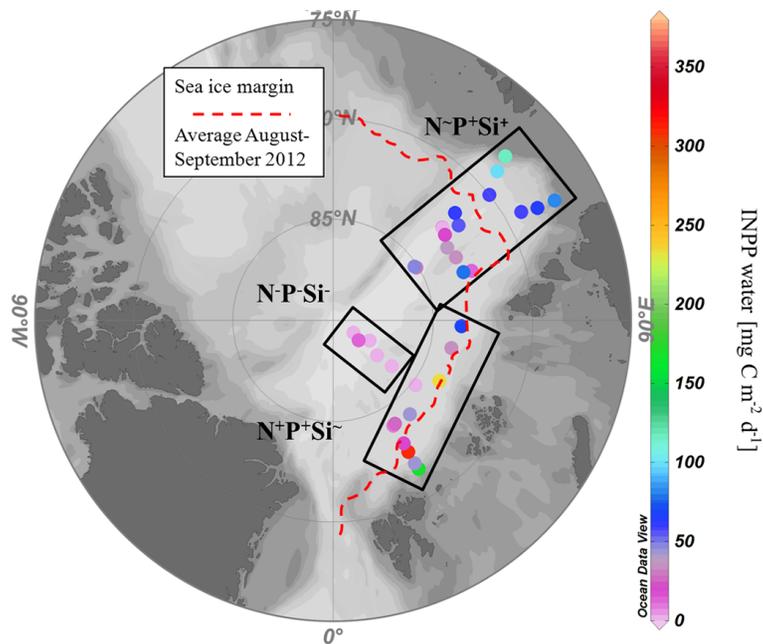


Figure 2. Integrated net primary productivity (INPP) in the water column of the Central Arctic Eurasian Basin in August–September 2012. The three boxes indicate different nutrient regimes characterized by the concentrations of nitrate (N), phosphate (P), and silicate (Si) in the water column. The superscripts on each nutrient indicate if there was high (+), medium (~) or low (–) amounts of that nutrient in the euphotic zone. High is defined as concentrations of nitrate > 3 μM nitrate, phosphate > 0.3 μM , and silicate > 3 μM . Low or depleted is defined as concentrations of nitrate < 1 μM , phosphate < 0.2 μM , and silicate < 1.5 μM .

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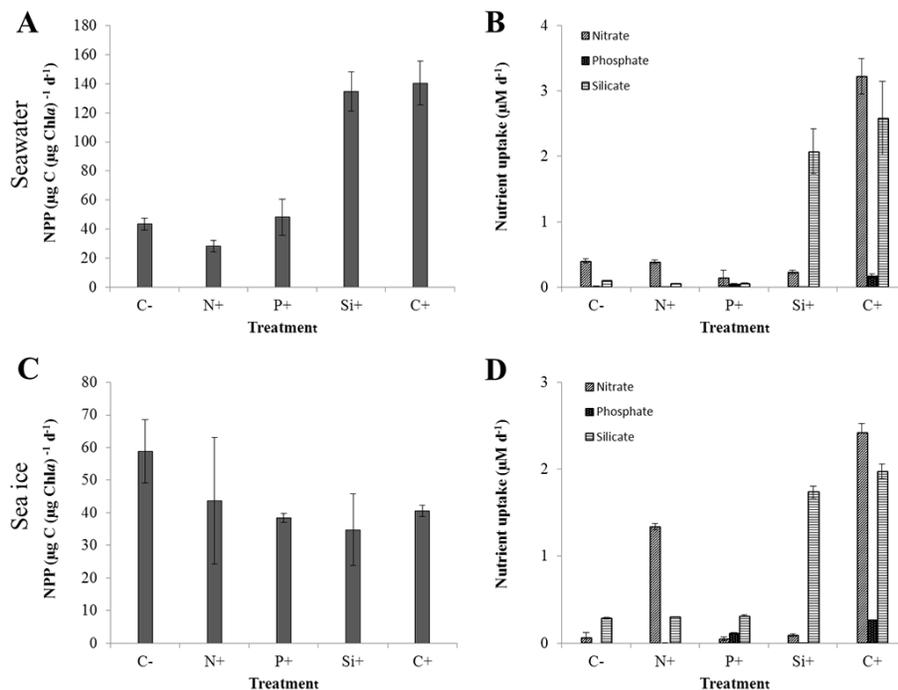


Figure 3. Nutrient addition experiments on sea water from Ice station 3 (**a** and **b**) and sea ice from Ice station 8 (**c** and **d**). Panels (**a**) and (**c**) show the NPP rate of each treatment after 24 h of nutrient addition. Panels (**b**) and (**d**) show the nutrient uptake in each treatment after nutrient addition. C⁻ negative control, N⁺ nitrate, P⁺ phosphate, Si⁺ silicate, C⁺ all nutrients added.

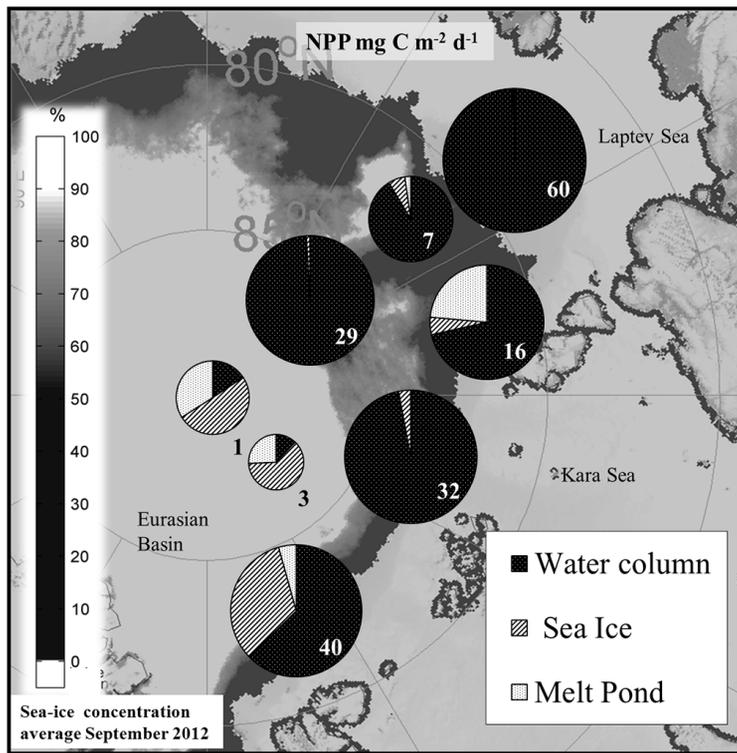


Figure 4. Depth integrated net primary productivity (INPP) and the contribution of sea ice, melt ponds and water at eight ice stations in the Eurasian Basin during summer 2012. The size of the pie chart represents the magnitude of INPP in $\text{mg C m}^{-2} \text{d}^{-1}$. The values are depicted next to each pie chart.

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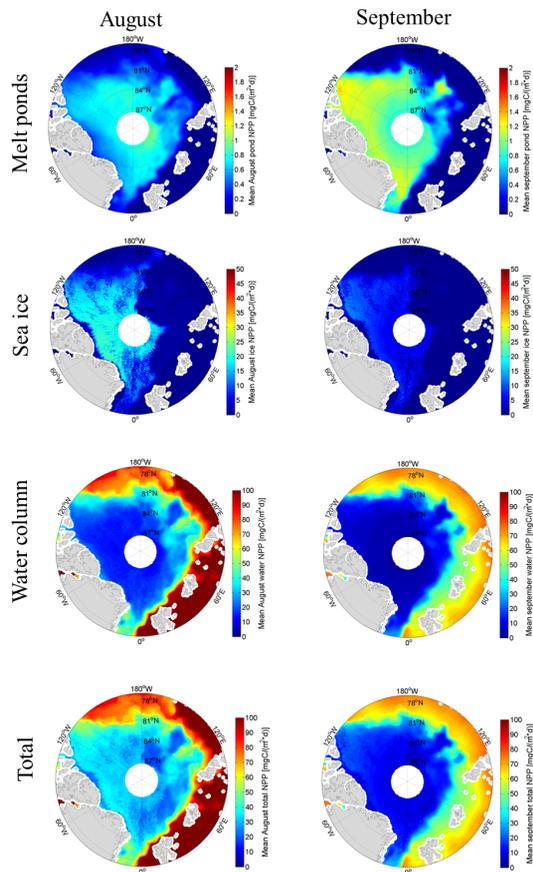


Figure 5. Total mean NPP and in each environment: melt ponds, sea ice and water in the Central Arctic during August and September 2012 as modeled with the CAOPP model.

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