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# Global Biogeochemical Cycles

## RESEARCH ARTICLE

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### Key Points:

- High under-ice export fluxes were observed on the northern Laptev Sea shelf
- Low under-ice export fluxes were observed above the central basin
- Nutrient supply is limiting export fluxes during summer above the central basin

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## Variability in under-ice export fluxes of biogenic matter in the Arctic Ocean

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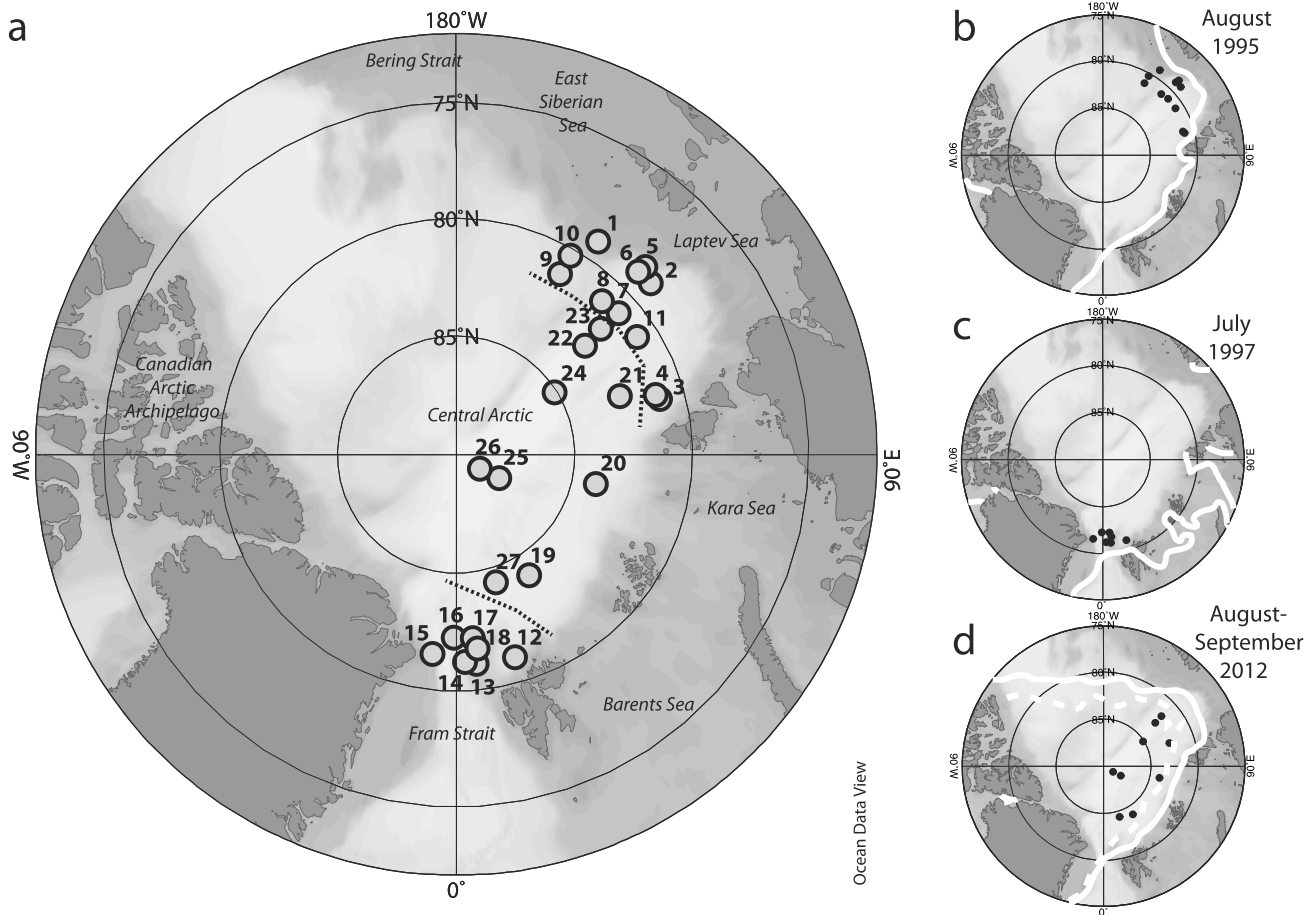
**Abstract** A critical question regarding the organic carbon cycle in the Arctic Ocean is whether the decline in ice extent and thickness and the associated increase in solar irradiance in the upper ocean will result in increased primary production and particulate organic carbon (POC) export. To assess spatial and temporal variability in POC export, under-ice export fluxes were measured with short-term sediment traps in the northern Laptev Sea in July–August–September 1995, north of the Fram Strait in July 1997, and in the Central Arctic in August–September 2012. Sediment traps were deployed at 2–5 m and 20–25 m under ice for periods ranging from 8.5 to 71 h. In addition to POC fluxes, total particulate matter, chlorophyll *a*, biogenic particulate silica, phytoplankton, and zooplankton fecal pellet fluxes were measured to evaluate the amount and composition of the material exported in the upper Arctic Ocean. Whereas elevated export fluxes observed on and near the Laptev Sea shelf were likely the combined result of high primary production, resuspension, and release of particulate matter from melting ice, low export fluxes above the central basins despite increased light availability during the record minimum ice extent of 2012 suggest that POC export was limited by nutrient supply during summer. These results suggest that the ongoing decline in ice cover affects export fluxes differently on Arctic shelves and over the deep Arctic Ocean and that POC export is likely to remain low above the central basins unless additional nutrients are supplied to surface waters.

## 1. Introduction

A synthesis of current knowledge on downward particulate organic carbon (POC) export in the Arctic Ocean indicates that export is high over the wide shallow continental shelves and low over the deep basins. This pattern was observed in several studies conducted over the last decades using <sup>234</sup>Th/<sup>238</sup>U disequilibrium or short-term drifting sediment traps to measure POC export [Wassmann *et al.*, 2004]. Indeed, higher POC export fluxes have been measured over the shelf than over the basin in the Bering Sea [Chen *et al.*, 2003], in the Chukchi Sea [Moran *et al.*, 1997; Lepore *et al.*, 2007], in the Beaufort Sea [Moran and Smith, 2000], and in the northern Barents Sea [Gustafsson and Andersson, 2012]. High POC export fluxes were also observed in northern Baffin Bay [Amiel *et al.*, 2002; Michel *et al.*, 2002] and in the Barents Sea [Coppola *et al.*, 2002; Olli *et al.*, 2002; Lalande *et al.*, 2008], while low POC export fluxes were reported over the deep Central Arctic Ocean [Olli *et al.*, 2007].

The ongoing decline in sea ice extent and thickness [Serreze *et al.*, 2007; Stroeve *et al.*, 2007; Haas *et al.*, 2008; Maslanik *et al.*, 2011; Comiso, 2012; Laxon *et al.*, 2013] and the associated increase in sunlight transmission due to larger meltpond coverage [Nicolaus *et al.*, 2012] are expected to cause unprecedented change in the biogeochemistry of the Arctic Ocean. Already, it was reported that the low sea ice extent recorded in 2007 led to an increase in marine primary production in Arctic waters, particularly over the Siberian shelves [Arrigo *et al.*, 2008], and to an increase in POC export fluxes over the continental slope of the Laptev Sea [Lalande *et al.*, 2009]. However, a comprehensive large-scale study of POC export using <sup>234</sup>Th/<sup>238</sup>U disequilibrium, also conducted in 2007, still displayed low POC fluxes over the central basins and enhanced POC export over the Arctic shelves, indicating that carbon sequestration was still limited under thinner sea ice over the deep basins [Cai *et al.*, 2010]. These results suggest that a decline in sea ice cover extent and thickness and an increase in light availability may enhance POC export on Arctic shelves and slopes only, and that the marked spatial variability in POC export in the Arctic Ocean is partly due to nutrient supply.

Nutrients enter the Arctic Ocean by inflows of Atlantic Water through Fram Strait and the Barents Sea, of Pacific Water through Bering Strait, and by rivers [Rudels *et al.*, 1991]. While Pacific Water and rivers supply



**Figure 1.** (a) Sampled stations in the northern Laptev Sea, north of Fram Strait, and in the Central Arctic. White lines indicate minimum sea ice extents in (b) 1995, (c) 1997, and (d) 2012; solid line = August; dashed line = September.

nutrients at shallow depths, the nutrient-rich Atlantic Water flows into the Arctic Ocean as a circumpolar subsurface boundary current moving cyclonically along the shelf break around the deep Arctic Ocean basin [Timofeev, 1960; Treshnikov and Baranov, 1972; Nikiforov and Shpaykher, 1980; Rudels, 2012]. A low salinity-cold surface layer prevents the Atlantic Water from reaching the surface unless mixing occurs. Therefore, nutrient supply is extensive on most of the large Arctic continental shelves, whereas strong stratification over the deep interior prevents the replenishment of nutrients [Tremblay and Gagnon, 2009]. This suggests that the central basins, representing nearly 40% of the Arctic Ocean, may not sustain elevated primary production, and hence elevated POC export fluxes, despite sufficient light conditions.

In this study, we present under-ice export fluxes measured with short-term drifting sediment traps at 27 stations in the Arctic Ocean during summer in 1995, 1997, and 2012 to further assess the spatial and temporal variability in POC export. The record low sea ice retreat in 2012 allowed the deployments of the sediment traps at higher latitudes but under similar ice conditions than 15 and 17 years earlier. In addition to POC, total particulate matter, chlorophyll *a*, phytoplankton cells, zooplankton fecal pellets, and biogenic particulate silica were measured to evaluate the spatial and temporal variability in the composition of the export fluxes in the upper Arctic Ocean.

## 2. Material and Methods

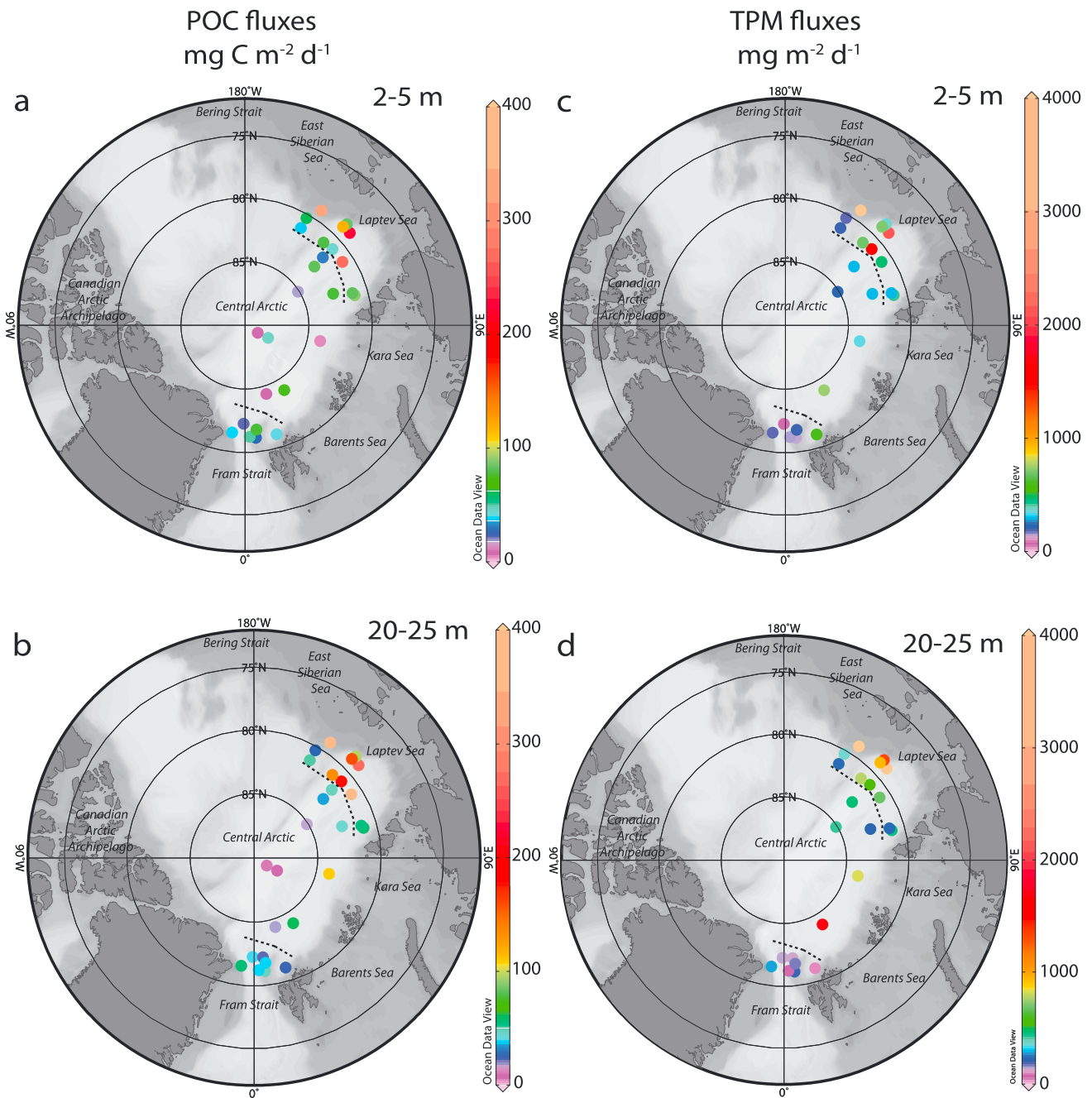
Short-term cylindrical sediment traps (HydroBios, Kiel, Germany) were deployed at 11 ice stations in the northern Laptev Sea in August 1995, at seven ice stations north of the Fram Strait in July 1997, and at nine ice stations in the Central Arctic in August–September 2012 during the ARKXI-1, ARKXIII-2, and ARKXXVII-3 expeditions on board *Polarstern* (Figure 1). At each station, sediment traps were deployed at 2 or 5 m and at

**Table 1.** Short-Term Sediment Traps Locations and Deployment Information

Region	Station	Date	Latitude (°N)	Longitude (°E)	Water Depth (m)	Deployment Time (h)
Northern Laptev Sea	1	7/28/1995	79.15	146.33	100	8.5
	2	8/4/1995	79.03	131.4	3150	16
	3	8/7/1995	81.08	105.32	2750	18
	4	8/8/1995	81.2	106.55	3250	25
	5	8/16/1995	78.72	134.73	2100	11
	6	8/17/1995	79.08	135.13	2750	18
	7	8/20/1995	80.88	131.05	3820	54
	8	8/22/1995	81.05	136.48	2800	16
	9	8/27/1995	81.2	150.08	2600	16
	10	8/28/1995	80.3	150.17	1600	18
	11	9/4/1995	80.87	123.02	3570	24
North of Fram Strait	12	7/6/1997	81.1	16.18	2077	23
	13	7/10/1997	81.12	5.57	649	23
	14	7/12/1997	81.23	2.4	1038	71
	15	7/16/1997	81.52	-6.8	2675	23.5
	16	7/19/1997	82.28	-0.72	2838	47.5
	17	7/22/1997	82.23	5.22	2927	48
	18	7/25/1997	81.77	6.32	1414	21
Central Arctic	19	8/10/2012	84.05	31.11	4013	25
	20	8/14/2012	83.99	78.10	3484	48
	21	8/20/2012	82.67	109.59	3569	47.4
	22	8/25/2012	82.88	130.13	4161	28.8
	23	9/4/2012	81.92	131.00	4031	25.4
	24	9/7/2012	85.10	122.25	4354	53.2
	25	9/18/2012	87.93	61.22	4380	25
	26	9/22/2012	88.83	58.86	4373	37.3
	27	9/28/2012	84.37	17.45	3513	24

20 or 25 m under a drifting ice floe for periods ranging between 8.5 and 71 h (Table 1). No poison was applied to the collecting cups during deployment. After recovery, the material collected was left to settle into the sampling cup at the bottom of the trap in a dark cold room for a period of ~6 h. Large swimmers were immediately removed with forceps when present, and poison ( $\text{HgCl}_2$ ; 0.14% final solution) was added to preserve the samples that were stored refrigerated until further processing in the laboratory.

In the laboratory, samples were split in subsamples for measurements of total particulate matter (TPM), chlorophyll *a* (Chl *a*), particulate organic carbon (POC), biogenic particulate silica (bPSi), phytoplankton cells, and zooplankton fecal pellets. Subsamples for TPM measurements were filtered onto preweighed GF/F filters (pore size: 0.7  $\mu\text{m}$ ), rinsed with distilled water to remove salt, dried at 60°C, and weighed again on a Mettler Toledo XP Excellence Plus microbalance. Subsamples for Chl *a* measurements were filtered onto GF/F filters that were extracted in 90% acetone and analyzed with the latest model of Turner Design fluorometer for each year sampled. Subsamples for POC measurements were filtered onto GF/F filters precombusted at 500°C for 4 h. Filters were soaked in 0.1 N HCl for removal of inorganic carbon and dried at 60°C. POC measurements were then conducted on a Carlo Erba CHN elemental analyzer. Subsamples for bPSi, a proxy for diatoms, were filtered on cellulose acetate filters (pore size: 0.8  $\mu\text{m}$ ), processed using the wet-alkaline method (pretreated 12 h at 85°C in an oven), and extracted for 2 h at 85°C in a shaking water bath [von Bodungen *et al.*, 1991]. This procedure principally extracts biogenic silica, and interference by lithogenic material is considered to be minimal. Subsamples were used for the enumeration of phytoplankton cells by inverted microscopy according to the *Utermöhl* [1958] method. A minimum of 50 to 100 phytoplankton cells of the dominant groups were counted at four magnifications (100, 160, 250, and 400 $\times$ ) using phase contrast microscopy. Only the dominant, identifiable, and intact cells were counted, except for rarely observed diatoms for which intact cells, empty frustules, and resting spores were counted. Before splitting the samples, zooplankton fecal pellets were enumerated (5–400 pellets depending on the sample) using a dissecting scope. The length and width of each fecal pellet (broken or intact) were measured, and pellet volumes were calculated according to the shape of the pellets. Cylindrical pellets were attributed to calanoid copepods, and ellipsoidal pellets were attributed to appendicularians [González *et al.*, 2000]. Fecal pellet volumes were converted to fecal pellet carbon (FPC) using a volumetric carbon conversion factor of 0.057 mg C  $\text{mm}^{-3}$  for copepod pellets and 0.042 mg C  $\text{mm}^{-3}$  for

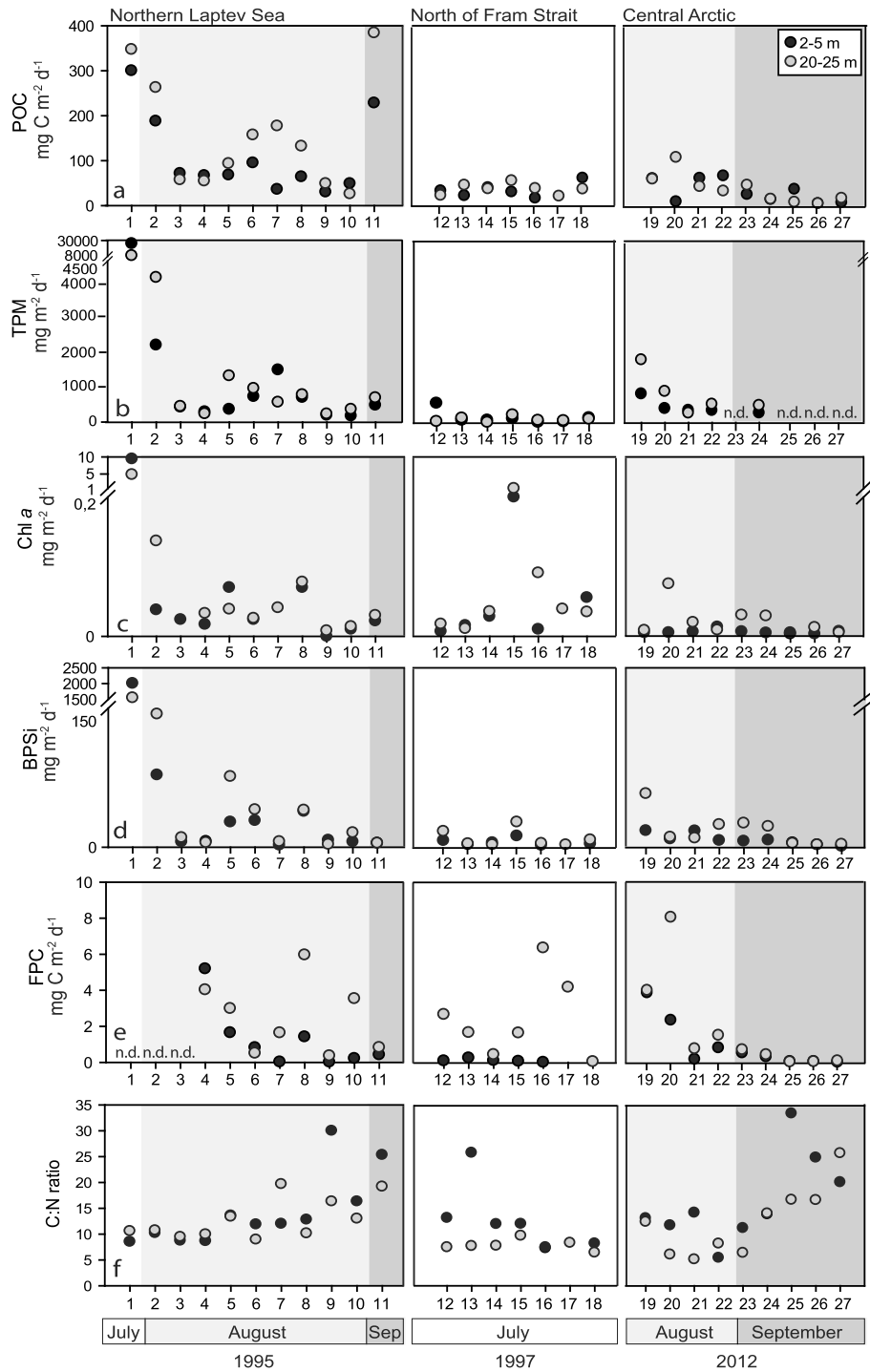


**Figure 2.** Under-ice POC export fluxes obtained at (a) 2–5 m and (b) 20–25 m, and under-ice TPM fluxes obtained at (c) 2–5 m and (d) 20–25 m in the Arctic Ocean. TPM fluxes were not available at some of the stations in the Central Arctic.

appendicularian pellets [González *et al.*, 1994; González and Smetacek, 1994]. TPM, Chl *a*, POC, bPSi, FPC, and phytoplankton cell measurements were converted to daily fluxes depending on deployment time for each station.

### 3. Results

Under-ice POC export fluxes reached high values in the northern Laptev Sea but remained lower than  $70 \text{ mg m}^{-2} \text{ d}^{-1}$  north of the Fram Strait and in the Central Arctic, except at station 20 ( $108 \text{ mg m}^{-2} \text{ d}^{-1}$  at 20–25 m; Figures 2a, 2b, and 3a). In the northern Laptev Sea, highest POC fluxes were observed at the end of July–beginning of August on or near the shelf (stations 1 and 2) and at the beginning of September farther over



**Figure 3.** Under-ice (a) POC fluxes, (b) TPM fluxes, (c) Chl *a* fluxes, (d) bPSi fluxes, (e) FPC fluxes, and (f) C:N ratios of the sinking particles obtained in the northern Laptev Sea from July to September 1995, north of Fram Strait in July 1997, and in the Central Arctic in August and September 2012. The white areas represent samples taken in the month of July, light gray areas samples taken in August, and dark gray areas samples taken in September. No data are available for some trap samples (n.d.).

the basin (station 11). In the region north of Fram Strait, POC fluxes were similar over the entire sampling region and the complete month of July, whereas POC fluxes decreased toward the end of September in the Central Arctic (Figures 2a, 2b, and 3a). Under-ice TPM fluxes were highest in the northern Laptev Sea and lowest north of Fram Strait (Figures 2c, 2d, and 3b). In the northern Laptev Sea, highest TPM fluxes were

observed at station 1 on the shelf, but TPM fluxes were also high at stations 2, 5, and 6 located closest to the shelf, and at stations 7 and 8 farther away from the shelf. In the Central Arctic, TPM fluxes were higher at the two first stations sampled in August (stations 19 and 20), while TPM fluxes at 20–25 m at stations 22 and 24 were similar than at the nearest stations sampled in the northern Laptev Sea. Under-ice TPM fluxes remained low at all stations north of Fram Strait (Figures 2c, 2d, and 3b).

Similar to POC and TPM fluxes, under-ice Chl *a* and bPSi fluxes were highest at the end of July at station 1 located on the shelf in the northern Laptev Sea (Figures 3c and 3d). However, in contrast to POC fluxes, Chl *a* and bPSi fluxes remained low at the beginning of September in the northern Laptev Sea. Chl *a* fluxes were also relatively high at station 15 located near the Greenland shelf north of Fram Strait but were associated with only slightly higher bPSi fluxes and low POC fluxes. In agreement with POC fluxes, Chl *a* and bPSi fluxes decreased toward the end of September in the Central Arctic (Figures 3c and 3d).

FPC fluxes displayed similar ranges in every region sampled, with no clear pattern except for a decrease in FPC fluxes toward the end of September in the Central Arctic (Figure 3e). C/N ratios of the exported biogenic matter increased at the end of August–beginning of September in the northern Laptev Sea and in September in the Central Arctic, while they displayed a stable pattern during July north of Fram Strait (Figure 3f). Under-ice export fluxes decreased, increased, or were identical between 2–5 m and 20–25 m among stations sampled but displayed a similar pattern among stations at both depths (Figure 3).

Phytoplankton cell fluxes were dominated by ice-associated pennate diatoms in the northern Laptev Sea and north of Fram Strait, while they were dominated by heterotrophic flagellates in the Central Arctic (Figure 4a). Pennate diatom fluxes, dominated by *Fragilariopsis* spp. and *Nitzschia frigida*, were highest at the end of July at station 1 located on the shelf in the northern Laptev Sea and in July at station 15 near the Greenland shelf north of Fram Strait (Figure 4a). Other common pennate diatoms belonged to the genera *Cylindrotheca*, *Pseudo-nitzschia*, and *Navicula*. The station near the Greenland shelf north of Fram Strait was the only station dominated by centric diatoms, which were mostly  $<10\ \mu\text{m}$  *Chaetoceros* spp. cells (Figure 4a). In the Central Arctic, flagellate fluxes (i.e., nanoflagellates and dinoflagellates) were highest at stations 22 and 23 located nearest to the northern Laptev Sea (Figure 4a).

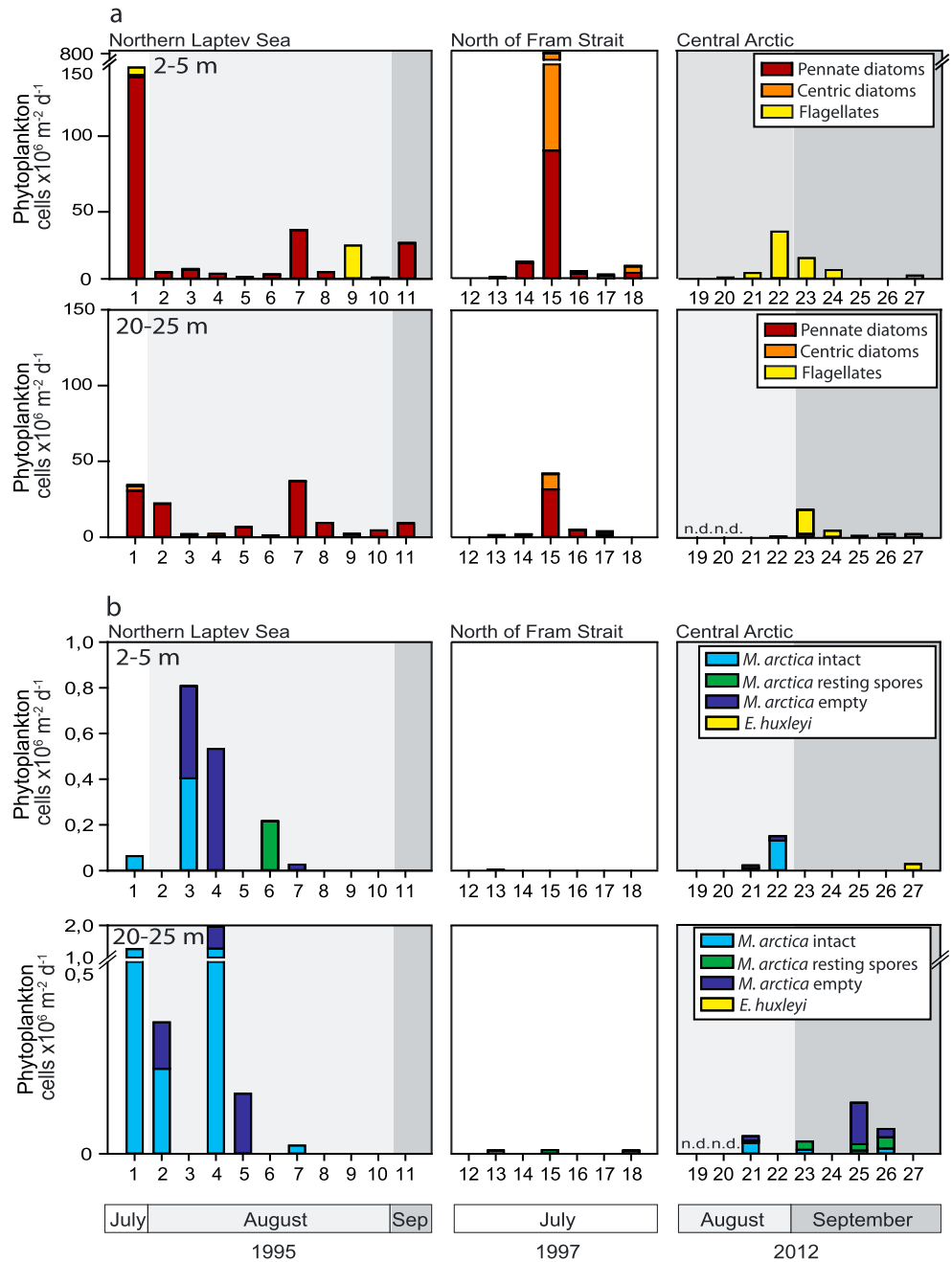
The ice-associated centric diatom *Melosira arctica* and the pelagic coccolithophore *Emiliania huxleyi* were observed at some of the stations (Figures 4b and 5). *M. arctica* intact cells, resting spores, or empty cells were present at all stations sampled from the end of July to mid-August in the northern Laptev Sea and at most stations in the Central Arctic but were nearly absent from the region north of Fram Strait except for some resting spores collected at station 15 near the Greenland shelf and at station 18, the last station sampled at the end of July (Figures 4b and 5). *E. huxleyi* was present at station 13 located in the region north of Fram Strait and at station 27 in the Central Arctic, the station closest to the north of Fram Strait (Figures 4b and 5).

## 4. Discussion

It is important to note that in addition to the methodological biases commonly associated with sediment traps [Buesseler, 1991; Gardner, 2000; Lalande et al., 2007b], the deployment of sediment traps under ice floes may introduce errors in flux measurements as ice floes may drift in different direction than surface currents due to wind forcing, preventing the traps to truly be free drifting. As ice drift direction and average drift speed may vary considerably during trap deployment, it is impossible to estimate how it affects under-ice trapping efficiency. Moreover, the wide range of deployment duration due to logistical constraints may have led to the overestimation of the daily export fluxes at stations with short deployment periods. Nevertheless, the large variation between export fluxes measured over the Laptev Sea shelf and over the basins, similar to observations made by Cai et al. [2010] from  $^{234}\text{Th}$ -derived flux measurements, suggests that export fluxes measured with ice-anchored drifting sediment traps are reliable despite these limitations.

### 4.1. Laptev Sea Shelf and Shelf Break

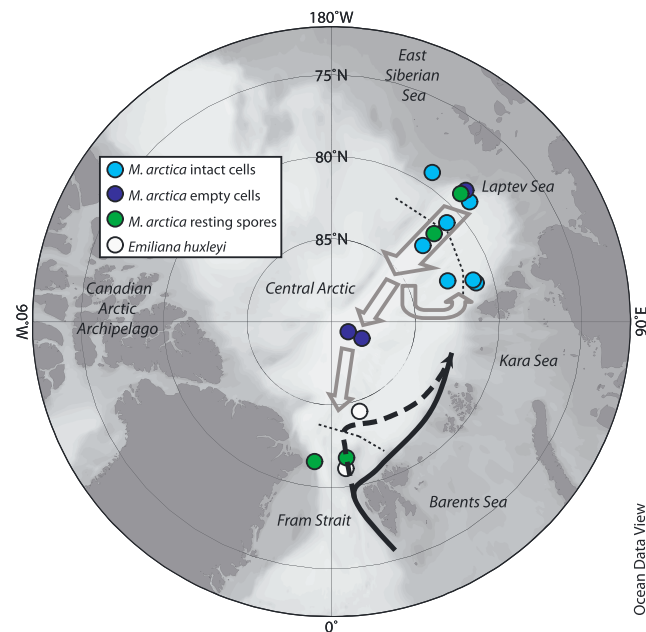
High under-ice export fluxes of POC, TPM, Chl *a*, diatoms, and bPSi at the end of July 1995 at station 1 located on the shelf in the northern Laptev Sea likely reflected a combination of high under-ice primary production, resuspension, and release of particulate matter from melting ice. However, the low C/N ratios of the sinking material at station 1 reflected the predominance of freshly produced particles, therefore indicating that under-ice primary production largely contributed to the elevated export fluxes. The dominance of the pelagic



**Figure 4.** (a) Phytoplankton cell fluxes and (b) phytoplankton cell fluxes of rarely observed species obtained in the northern Laptev Sea from July to September 1995, north of Fram Strait in July 1997, and in the Central Arctic in August and September 2012. The white areas represent samples taken in the month of July, light gray areas samples taken in August, and dark gray areas samples taken in September. No data are available for some trap samples (n.d.).

pennate diatom *Achnanthes taeniata* and of the ice-associated pennate diatom *Nitzschia frigida* in the phytoplankton cell fluxes (data not shown) suggest that high under-ice primary production at that station was due to the co-occurrence of an under-ice bloom and enhanced ice algae release on the shelf. The elevated export fluxes of Chl *a*, diatoms, bPSi, and POC indicate that the shallow northern Laptev Sea may experience higher primary production than previously estimated [Carmack and Wassmann, 2006] and suggest that productivity has been underestimated in this remote and rarely sampled region. Indeed, the high POC fluxes on the Laptev Sea shelf were in the same range as POC fluxes obtained at similar depths during an under-ice phytoplankton bloom in the Canadian Arctic Archipelago [Fortier et al., 2002] and in the





**Figure 5.** Stations where *Melosira arctica* and *Emiliana huxleyi* were present. Gray arrows represent the Transpolar Drift. Black arrow represents the Atlantic Water inflow into the Arctic Ocean, along with the Yermak Plateau branch (dash line) of the Atlantic Water inflow.

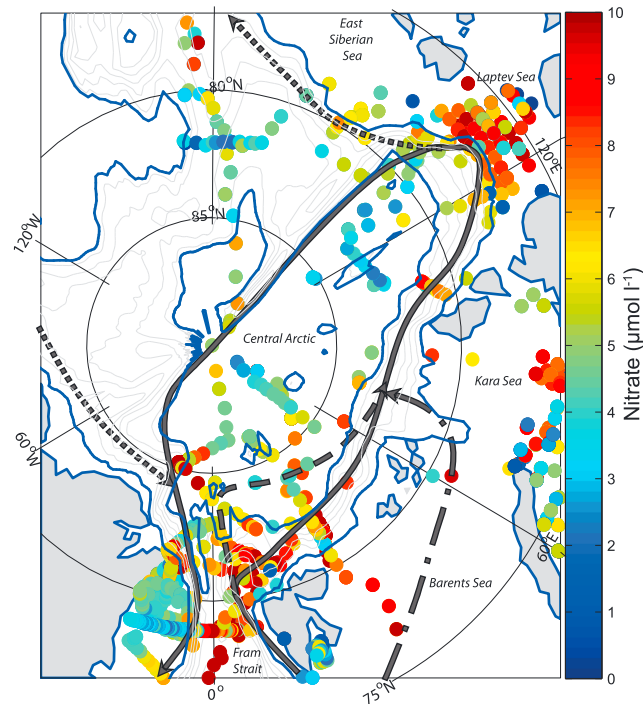
rich Atlantic-derived waters onto the shelf [Dmitrenko *et al.*, 2010; Janout *et al.*, 2013]. However, the consistently high nitrate concentrations observed below the mixed layer on the northern Laptev Sea shelf (Figure 6) and the large tidal amplitudes recorded on the outer Laptev Sea shelf [Janout and Lenn, 2013] rather suggest that remineralized nutrients supplied to the surface layer through vertical mixing led to the elevated export fluxes observed at the outer Laptev shelf. Resuspension induced by the strong tidal mixing on the shallow outer shelf also contributed to the extremely high TPM fluxes observed at station 1 near the Laptev Sea shelf break. Away from the shelf, the elevated POC and TPM fluxes observed at several stations in the northern Laptev Sea were probably the combined result of increased primary production caused by the advection of nutrients with surface waters from the shelf, advection of resuspended material from the shelf, and release of particulate matter from the melting sea ice. Indeed, a large quantity of suspended particulate matter is incorporated into newly formed ice during freeze-up on the shallow Laptev Sea shelf, transported over the continental margin into the deep Arctic Ocean by strong southerly winds, and dispersed through the Central Arctic with the Transpolar Drift [Wegner *et al.*, 2005]. Elevated POC and TPM fluxes at stations located along the Transpolar Drift, along with low POC and TPM fluxes across the Lomonosov Ridge and nearest the Severnaya Zemlya Archipelago, support the release of particulate matter from melting ice as the predominant mechanism for the export of particulate matter from the Laptev Sea shelf.

#### 4.2. Central Arctic Basin

In contrast to the high under-ice fluxes measured on and near the Laptev Sea shelf, under-ice POC, Chl *a*, and bPSi fluxes were low over the deep basins. This spatial variability in sediment trap-derived POC fluxes concurs with the spatial variability of  $^{234}\text{Th}$ -derived POC fluxes measured in 2007 in the Central Arctic Ocean [Cai *et al.*, 2010]. Under-ice POC fluxes over the deep basins were also similar to under-ice POC fluxes obtained at 88–89°N during a drifting sediment trap study conducted in August 2001 in the Central Arctic Ocean [Olli *et al.*, 2007]. These results indicate that while the Arctic Ocean experienced exceptional melt pond occurrence in recent years [Rösel and Kaleschke, 2012], POC export fluxes did not increase over the deep basins. The consistently low POC fluxes under increased sunlight transmission over the Arctic basins suggest that POC export is not limited by light availability and is likely to remain low under further ice retreat and thinning. Following their ice-drift experiment in the Central Arctic Ocean in August 2001, Olli *et al.* [2007] proposed

very productive Barrow Canyon of the Chukchi Sea [Lalande *et al.*, 2007a]. The elevated export fluxes of Chl *a*, diatoms, and bPSi reflecting high under-ice primary production in the northern Laptev Sea in 1995 also suggest that the high primary production reported from satellite-derived measurements in the Laptev sector of the Arctic Ocean during the important sea ice retreat of 2007 [Arrigo *et al.*, 2008] was not reflecting an increase in primary production but represented instead the first satellite measurement of this high productivity, as much of this area had never been ice free for as long as satellite measurements have been available.

The location of the highly productive station near the Laptev Sea shelf break suggests that the under-ice phytoplankton bloom and the elevated ice algae production may have been partly fueled by the bottom onshore transport of warm, saline, and nutrient-



**Figure 6.** Nitrate concentrations below the mixed layer (30–60 m) in the Arctic Ocean. Nitrate values were obtained in summer (July, August, or September) from 1980 to 2007 and during the ARKXXVII-3 expedition in 2012. All data from 1980 to 2007 are available in the PANGAEA database ([www.pangaea.de](http://www.pangaea.de)). The 500 and 3000 m depth isobaths are highlighted (blue lines). The gray arrows represent the circulation of the Atlantic Water in its different branches in the Arctic. The solid line indicates the Fram Strait branch circumnavigating the Eurasian Basin. The split of the Atlantic Water flow into a branch crossing the Lomonosov Ridge and flowing along the Amerasian Basin shelf break is also shown (dot line). The Barents Sea (dash dot line) and Yermak Plateau (dash line) branches are also shown.

bloom, as reflected by the high export fluxes of *Chl a* and of pelagic centric diatoms dominated by *Chaetoceros* spp. (Figures 3c and 4a). However, the occurrence of this under-ice bloom did not result in elevated POC fluxes, and the processes regulating POC export north of Fram Strait remain unknown. The observation of under-ice blooms on the Laptev Sea shelf and near the Greenland shelf during this study further suggests that under-ice blooms are widespread across the Arctic Ocean [Mundy et al., 2009; Arrigo et al., 2012] following observations in the Barents Sea [Strass and Nöthig, 1996], Canadian Arctic Archipelago [Fortier et al., 2002], Beaufort Sea [Mundy et al., 2009], and Chukchi Sea [Arrigo et al., 2012].

The spatial variability in the magnitude and composition of the phytoplankton cell fluxes also supports nutrient supply as an important factor limiting primary production and export in the Arctic Ocean. High diatom fluxes were observed at the shallowest stations located on the Laptev Sea shelf and near the Greenland shelf, while low cell fluxes in flagellate-dominated waters were observed above the central basin. These results are in agreement with a recent study showing that phytoplankton communities in the Canadian High Arctic are shaped by vertical mixing and nutrient input, with flagellates dominating oligotrophic systems and diatoms dominating eutrophic systems [Ardyna et al., 2011]. Moreover, the spatial distribution of *E. huxleyi* and *M. arctica* provided information on water mass distribution and ice drift in the Arctic Ocean (Figure 5). *E. huxleyi* blooms, typically reported in warmer waters of the northern North Atlantic and the Norwegian Sea, were recently observed further north due to the subsurface circumpolar boundary current carrying water of Atlantic origin west of Svalbard and then eastward along the Eurasian shelf break [Hegseth and Sundfjord, 2008; Lalande et al., 2011]. The presence of *E. huxleyi* at a station northwest of Svalbard in July 1997 (Figure 5) suggests that the intrusion of this Atlantic phytoplankton species in the high Arctic occurred earlier than 2003, as previously reported by Hegseth and Sundfjord [2008]. The presence of *E. huxleyi* at

that the low under-ice POC fluxes during the peak of the productive season resulted from the excess grazing pressure of the large copepods expatriated into the Central Arctic Ocean. However, the higher under-ice POC, *Chl a*, and FPC fluxes measured concurrently with a higher nitrate value at station 20 than at the other stations sampled over the basins suggest instead that nutrient supply is the principal factor limiting export in the Central Arctic (Figures 3a, 3c, and 3e). Station 20 was located above the end of the slope, where the position of the Atlantic Water boundary current induces the formation of a convergent front. An episode of freezing conditions at the time of sampling caused convective mixing and the entrainment of nutrients from the subsurface Atlantic Water inflow to the upper layer (Figure 6). Although high nitrate values were also observed north of Fram Strait (Figure 6), POC export fluxes in this region remained low (Figures 2a, 2b, and 3a). This disparity may be due to an almost complete absence of stratification in the region (data not shown), except at station 15 located near the Greenland shelf where stratified conditions likely promoted the development of an under-ice

another station located farther north of Fram Strait in 2012 indicates that further intrusion of this warmer waters species is occurring in the Central Arctic, presumably with the Yermak Plateau branch of the Atlantic Water inflow (Figure 5). In addition, the diatom *M. arctica* was observed at more than half of the stations sampled over the 3 years (Figure 5). Since the first report of *M. arctica* from the Norwegian North Polar Expedition on board *Fram* [Nansen, 1897; Gran, 1904], *M. arctica* has been observed in nearly all sea ice-covered regions of the northern hemisphere; from the Okhotsk Sea [McMinn *et al.*, 2008], Baltic Sea [Norrman and Andersson, 1994; Haecky *et al.*, 1998], and the northern part of the Gulf of St Lawrence [Bérard-Therriault *et al.*, 1999] in subarctic regions, to the Chukchi Sea [Quillfeldt *et al.*, 2003; Ambrose *et al.*, 2005], Laptev and East Siberian Seas [Okolodkov, 1992; Zernova *et al.*, 2000], Beaufort Sea [Róžańska *et al.*, 2008; Niemi *et al.*, 2011], Barents Sea [Hegseth, 1992; Falk-Petersen *et al.*, 1998], northeast Greenland [Gutt, 1995], Northeast Water Polynya [Bauerfeind *et al.*, 1997], Fram Strait [Gradinger and Baumann, 1991], and the Central Arctic Ocean [Booth and Horner, 1997; Gosselin *et al.*, 1997; Melnikov *et al.*, 2002]. In our study, the high fluxes of intact *M. arctica* cells at stations located on and near the Laptev Sea shelf, the lower fluxes of intact *M. arctica* cells and the higher fluxes of empty *M. arctica* cells at a few stations in the Central Arctic, and the presence of *M. arctica* resting spores only in the region north of Fram Strait suggest that *M. arctica* cells are produced on the Laptev Sea shelf and dispersed through the Central Arctic with the Transpolar Drift (Figure 5), similar to the basin-wide dispersal of sediments by sea ice [Eicken *et al.*, 2000].

The large dispersal of particulate matter released from melting ice along the Transpolar Drift was reflected by similar TPM fluxes measured at nearby stations in the northern Laptev Sea (stations 7, 8, and 11) and in the Central Arctic (stations 22 and 23; Figures 2c and 2d). The lowest TPM fluxes measured north of Fram Strait suggest that most of the ice-exported particulate matter was released before reaching this region. The elevated TPM fluxes obtained at stations located away from the Transpolar Drift (stations 19 and 20) in the Central Arctic most likely reflected the release of ice-exported particulate matter from the nearer Kara and Barents Sea shelves (Figures 2c, 2d, and 3b).

### 4.3. Temporal Variability in Export Fluxes

Although export fluxes were measured over a 17 year interval, sampling was limited to a 3 month period in summer, as is typical for Arctic Ocean studies due to difficult access of this remote area at other times of the year. At the time of sampling, primary production has already taken place for several weeks, rapidly exhausting the nutrient reservoir in areas without continuous nutrient supply. This implies that the amount and composition of the material exported are probably different earlier in the productive season. This is clearly illustrated by the observation in August–September 2012 of a widespread deposition of *M. arctica* strands on the deep seafloor of the Arctic basins [Boetius *et al.*, 2013]. Most of this massive algal flux was estimated to have occurred before June [Boetius *et al.*, 2013], suggesting that under-ice POC export fluxes may have been higher if measured a few weeks earlier. Large amounts of *M. arctica* cells were also collected in long-term sediment trap samples obtained at 150 m over the Lomonosov Ridge in the Central Arctic (near station 8) during summer 1996 [Zernova *et al.*, 2000; Fahl and Nöthig, 2007], indicating that the widespread deposition of *M. arctica* observed in 2012 was a recurrent event rather than the result of a recent decline in ice cover. In 1996, the export of *M. arctica* and other ice algae started at the beginning of June, peaked at the end of July, and persisted until the end of the long-term deployment in August [Zernova *et al.*, 2000]. These results further indicate that a considerable fraction of biogenic matter is exported before August in the Central Arctic and that export fluxes would have been higher if measured earlier in the season, underscoring the necessity for long-term measurements during spring and early summer in the Arctic Ocean to properly assess the impact of the ongoing decline in ice cover.

The temporal variation in export is further illustrated by the change in the amount and composition of the fluxes during sampling in the northern Laptev Sea in 1995. Over the 39 day sampling period, Chl *a*, bPSi, diatom, and *M. arctica* fluxes decreased while C:N ratios of the exported material increased (Figures 3a, 3c, 3d, 3f, and 4b), reflecting a transition from the export of a diatom bloom at station 1 sampled in July to the export of a large fraction of visually unrecognizable amorphous detritus at station 11 sampled in September. A similar decrease in export was observed during sampling in the Central Arctic in 2012, with increasingly low fluxes of refractory material toward the end of the 51 day sampling period. Thus, the low POC fluxes obtained at the northernmost stations sampled during freezing conditions in September 2012 (stations 25 and 26) may

have been higher if sampled earlier in the season. In addition, although FPC fluxes showed no clear pattern except for a decrease toward the end of September in the Central Arctic, zooplankton grazing may have affected the amount and composition of export fluxes differently earlier in the productive season. Again, these temporal variations demonstrate the necessity for long-term measurements, especially during spring and early summer, to better understand biogeochemical fluxes in the Arctic Ocean.

## 5. Conclusions

Under-ice export fluxes obtained during 3 years over a 17 year interval and over a wide region in the Arctic Ocean showed enhanced export over and near the Laptev Sea shelf and reduced export over the central basins, similar to the spatial variation in POC export observed 5 years earlier in the Central Arctic Ocean [Cai *et al.*, 2010]. The lack of increase in export fluxes above the central basins during the record ice minimum of 2012, when light transmission increased through thinner ice and higher meltpond coverage, indicates that export is not limited by light during summer in the Central Arctic. Instead, our results suggest that although export in the Central Arctic is influenced by the Transpolar Drift, nutrient supply is the primary factor controlling biological productivity and export over the central basins during summer. These results support the suggestion that an increase in irradiance should have weak or no effect in oligotrophic regions [Ardyna *et al.*, 2011]. This implies that although further thinning of Arctic ice is expected [Vinnikov *et al.*, 1999; Laxon *et al.*, 2013; Rothrock *et al.*, 2003; Perovich and Richter-Menge, 2009], nearly 40% of the Arctic Ocean may not sustain an increase in primary production and export despite increased solar irradiance, unless additional nutrients are supplied to surface waters [Arrigo and van Dijken, 2011].

Also, the high under-ice export fluxes observed under favorable mixing conditions on the outer Laptev Sea shelf suggest that this region may be an important area of carbon export to the basin and/or benthos. As the resuspension of remineralized nutrients induced by strong tidal mixing is potentially occurring in other regions along the shallow Siberian shelf, high export areas are probably present elsewhere in the Eurasian Arctic. The elevated under-ice fluxes observed in the northern Laptev Sea also reinforce the indication that a considerable amount of under-ice primary production is not detected by remote sensing [Tremblay *et al.*, 2011, 2012].

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