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Phytoplankton distribution in unusually low sea ice cover over the Pacific Arctic

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Abstract

A large part of the Pacific Arctic basin experiences ice-free conditions in summer as a result of sea ice cover steadily decreasing over the last decades. To evaluate the impact of ice retreat on the Arctic ecosystem, we investigated phytoplankton communities from coastal sites (Chukchi shelf) to northern deep basins (up to 86° N), during year 2008 of high melting. Pigment and taxonomy in situ data were acquired under different ice regime: the ice -free basins (IFB, 74°–77° N), the marginal ice zone (MIZ, 77°–80° N) and the heavy ice covered basins (HIB, >80° N). Our results suggest that extensive ice melting provided favorable conditions to chrysophytes and prymnesiophytes growth and more hinospitable to pico-sized prasinophytes and micro-sized dinoflagellates. Larger cell diatoms were less abundant in the IFB while dominant in the MIZ of the deep Canadian basin. Our data were compared to those obtained during more icy years, 1994 and to a lesser extent, 2002. Freshening, stratification, light and nutrient availability are discussed as possible causes for observed phytoplankton communities under high and low sea ice cover.

1 Introduction

Both sea ice extent (10% per decade for 1979–2006, Comiso et al., 2008; Poliakov et al., 2010) and thickness (loss over 50% of its ice volume, Kwok and Rothrock, 2009) have shown significant decrease in the recent years, reaching lowest values in 2007 and 2011 (Perovich, 2011). Concomitantly, river discharge increased (Peterson et al., 2006) leading to freshwater accumulation in the upper Arctic Ocean (Rabe et al., 2011), which is strongest in the Pacific sector of the Arctic Ocean also impacted by the Pacific Water inflow (Proshutinsky et al., 2009; Woodgate et al., 2005). Environmental parameters driving phytoplankton growth such as light, stratification, surface water freshening, temperature and nutrients availability have thus been modified and led to changes of Arctic primary producer distributions (Grebmeier, 2010; Wassmann et al.

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2010). Increased phytoplankton primary production (PP) and total biomass in marginal Arctic seas are suggested by mathematical models (Zhang et al. 2010; Slagstad et al., 2011) and in situ data from the Beaufort Sea (Carmack and Chapman 2003; Lee and Whittedge, 2005), and the Barents and Greenland seas (Rysgaard et al., 1999).

5 Satellite observations also concluded to increased PP in the Arctic basin (Arrigo et al. 2008; Pabi et al., 2008).

In Arctic shelf waters, higher PP would result from increased light due to smaller ice cover and higher nutrient availability fed by wind-driven upwellings (Carmack et al., 2004; Yang et al., 2004), favoring the development of larger taxa such as diatoms (Babin et al., 2004). A longer phytoplankton growing season and the propagation of ice-edge blooms as the melt season lengthens would also contribute to enhance PP (Perette et al., 2011). However, the response of the Arctic phytoplankton is not uniform and shows differences in shallow seas and Arctic deep basin waters. Recent studies in the deep Canada Abyssal Plain reported no PP increase in ice-free waters (Cai et al., 2010; Joo et al., 2012). Other works suggest a shift towards smaller sized phytoplankton (Li et al., 2009). A northward displacement of sub-Arctic species such as coccolithophores in the Barents Sea (Hegseth and Sundfjord, 2008) or the occurrence of Pacific diatom *Neodenticulla seminae* have also been observed (Reid et al., 2007).

Impact of ice melting on the Arctic phytoplankton differs among species, varying widely across the Arctic. High latitudes deep basins covered by ice throughout the year are often dominated by ice-associated algae (Gosselin et al., 1997) such as the centric diatoms *Melosira arctica* (Gradinger, 1999; Melnikov et al., 2002) while picoplankton, mainly the prasinophyte *Micromonas* sp., dominates the water column phytoplanktonic community (Lovejoy et al., 2006, 2007). Lower latitude shallow shelves free of ice in summer indicate high PP rates consisting of large-cell pelagic species dominated by pennate and centric diatoms, and dinoflagellates (Poulin et al., 2011). Highest production occurs in spring as “ice edge blooms” over the shelves (Sakshaug and Skodjal, 1989), and is mainly due to centric colonial diatom genera *Chaetoceros* and *Thalassiosira* and prymnesiophyte *Phaeocystis pouchetii* (Wassmann, 1999). In contrast,

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pre- and post-bloom periods are dominated by small cells, such as small prymnesiophytes, and picoplankton (Hodal and Kristiansen, 2008). Because phytoplankton communities are differently affected by ice retreat, a comprehensive understanding of the Arctic ecosystem evolution requires knowledge at a local scale. Alteration of the phytoplankton population structure has consequences on the marine food web and nutrient cycling (Tremblay et al., 1997; Laws et al., 2000; Beardall and Raven, 2004) and subsequent Carbon fixation and export to the deep sea (Sigman and Boyle, 2000), which ultimately affect the CO₂ Arctic sink (Bates et al., 2006; Anderson et al., 2010; Cai et al., 2010).

To address these issues, phytoplankton observations after ice melting need to be acquired together with environmental parameters. Phytoplanktonic pigments and taxonomy enumerations are reported here for the first time in large areas of the deep basins of the Pacific Arctic, free of ice in 2008, i.e. in the less documented while most affected area by ice melting (Grebmeier, 2010). Taxonomic data are compared with those acquired in the same sector of the Arctic, along the Arctic Ocean Section (AOS) in summer 1994, when sea ice was much thicker above the entire basins (Booth and Horner, 1997; Sherr et al., 1997 and Gosselin et al., 1997). Pigment data over ice-free shelf and slope are compared with those obtained in 2002, under partially ice-covered conditions.

2 Methods

2.1 Study area

The CHINARE 2008 oceanographic cruise was conducted onboard the Chinese icebreaker R/V *Xuelong*, from 1 August to 8 September 2008, in the Pacific Arctic Ocean from 65° N to 86° N (Fig. 1a). The study area has been divided into two geographical provinces based on bathymetric features: the shallow Chukchi shelf (<100 m) and the deep basins (100 to 4000 m). The deep basins include the Canada Abyssal Plain, the

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Alpha Ridge, the Mendeleev Abyssal Plain (MAP) and the Chukchi Borderland. The Chukchi Borderland, considered as a mid-depth (~1000 m) extension of the Chukchi shelf, is composed of the deep Chukchi Abyssal Plain (CAP) and the Chukchi Cap (CC). The Canada Abyssal Plain ends in the South by an abrupt shelf-break, while the Northwind Ridge (NR) forms its western boundary and the Alpha Ridge (AR) its northern boundary.

Waters of the Canada Arctic are characterized by an exceptionally wide range of salinity, from 24 to 35, and temperatures varying from near-freezing point to 7°C (Fig. 1b). The ubiquitous Arctic Polar Mixed Layer (PML; Codispoti et al., 2005) occupies the 5–25 m depth range and show highly variable temperature and salinity values. Below the PML down to 200 m depth, the water column exhibits a strong salinity gradient, which characterizes the halocline layer (Aagaard et al., 1981). Below the halocline, down to 300 m, the thermocline layer is characterized by a pronounced temperature and salinity gradients ($34.0 < S < 34.8$, $-0.7 < \theta < 0^\circ\text{C}$) marking the transition between the halocline and the Atlantic Water ($34.5 < S < 34.9$, $\theta > 0^\circ\text{C}$), lying between 300 and 1000 m. The Arctic Deep Waters ($S \sim 34.95$, $\theta < 0^\circ\text{C}$) occupy the water column below 1000 m. The Pacific Water (PW, $31 < S < 33.5$; Woodgate et al., 2005) penetrates into the Arctic Ocean through the Bering Strait. While, the PSW (Pacific Summer Waters) become depleted in nutrients during its passage across the Bering Sea, the PWW (Pacific Winter Waters) are enriched in nutrients (Aagaard and Roach, 1990; Weingartner et al., 1998). The PW, lying between 20 and 60 m on the shelf and between 50 to 200 m in deep basins, represent a substantial reservoir of nutrients (NO_3 : 10–15 μM ; Si: 20–40 μM) for the upper Arctic Ocean. The silicate signal of the PWW are observed at all stations up to 85° N, whereas the PSW are seen exclusively over the shelf and in the southern Canadian Abyssal Plain.

Phytoplankton distributions in the water samples collected during the CHINARE 2008 cruise were determined from microscopic enumerations of individual species and pigments analyzed by high-performance liquid chromatography (HPLC) (Jeffrey et al., 1997). Species composition previously described by Joo et al. (2012) are combined

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to pigment data to more robustly characterize phytoplanktonic communities and be compared to earlier published data obtained under different summer sea ice cover conditions.

2.2 HPLC pigments

5 Samples for pigment analyses were collected at 65 stations (Fig. 1a) and 2 depths, i.e. in surface waters (3 m) and in the sub-surface chlorophyll maximum (SCM) located from in situ fluorescence profiles. About 2 l of seawater were filtered through 25 mm Whatman GF/F filters (0.7 μm porosity), then stored in a freezer at -80°C to avoid biological degradation. HPLC analyses were performed in SOA (Second Institute of Oceanography, Hangzhou, China) following the method developed by Van Heukelem and Thomas (2001). Pigments were extracted for 1 h at -20°C in methanol and placed in an ultra-sonic bath to disrupt cells. An internal standard, the DL- α Tocopherol acetate, was added to the solvent extracts to correct pigment concentrations from recovery. Pigments were analyzed using a Waters 600E HPLC and an Eclipse C8 column (150 \times 4.6 mm, 3.5 μm) thermostated at 60°C at a flow rate of 1 ml min $^{-1}$. Every 30 samples, a standard mixture was analyzed under the same conditions as the samples. Chlorophyll-*a* (chl-*a*) and chlorophyll-*b* (chl-*b*) standard concentrations were determined by spectrofluorometry using published extinction coefficients (Jeffrey and Humphrey, 1975). Chl-*a* and 17 accessory pigments were quantified based on their retention time (see Supplementary Table 1). The proportion of each pigment relative to the total pigments was used to estimate the phytoplankton composition (Jeffrey and Veski, 1997).

The relative contribution of different phytoplankton classes to the total chl-*a* concentration was obtained using the matrix factorization program CHEMTAX (CHEMical TAXonomy) running under MATLABTM following Mackey et al. (1996). Twelve pigments were used to distinguish between eight phytoplankton classes and three size classes: microphytoplankton ($>20\ \mu\text{m}$), nanophytoplankton (2–20 μm) and picophytoplankton ($<2\ \mu\text{m}$) (see Supplementary Table 1).

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2.3 Light microscopy identification, counts and biomass of phytoplankton

26 stations were sampled for taxonomy enumerations at the same two depths as for pigment analyses (Fig. 1a). About 100 ml of water taken from Niskin bottles were used for microscopic identification and preserved with glutaraldehyde (final concentration 1 %) before filtration through Gelman GN-6 Metricel filters (0.45 μm pore size, 25 mm diameter). The filters were mounted on microscope slides with water-soluble embedding media (2-hydroxypropyl methacrylate) onboard. In the laboratory, the slides were used to identify and count phytoplankton species following the procedure of Lee et al. (2012). At least 300 cells were counted under the microscope (BX51, Olympus) with a combination of light and epifluorescence microscopy at 400 \times for microplankton and at 1000 \times for pico- and nanoplankton. The carbon biomass associated to each phytoplanktonic group was estimated from species specific biovolumes according to the equations of Menden-Dauer and Lessard (2000). Biovolume estimates of each species were based on cell dimensions measured by light microscopy using appropriate geometric shapes according to Sun and Liu (2003).

3 Results

3.1 Physical and biogeochemical parameters

Ice cover; temperature, salinity, euphotic depth, nitrate concentrations, nutricline depth and bathymetry are shown in Fig. 2.

Ice cover. Except for a tongue of ice (ice \sim 50 %) between 72° and 74° N, the Chukchi shelf was free of ice (Fig. 2a). South of 77° N the ice cover was less than 20 %, a value which characterizes the “ice-free basins” (IFB, ice <20 %). Ice concentration was highly variable (20–70 %) in the “marginal ice zone” (MIZ), over the Chukchi Borderland and the Canada Abyssal Plain. In the latter called “heavy-ice basins” (HIB), the ice cover was >70 %, reaching exceptionally 90 % or more, at three stations North of 84° N.

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Temperature and Salinity. The surface temperature reached 6°C South of the Chukchi Plateau a region free of ice and thus exposed to light radiation for longer periods (Fig. 2b). Over the deep basins, in the southern Canada Abyssal Plain, temperatures in the ice-free surface waters were 2°C warmer than the near freezing values in ice-covered areas (-1.4 ± 0.1 °C). Surface salinity was relatively low throughout the study area (28.1 ± 2.2 , Fig. 2b), reflecting freshwater inputs from sea ice melting and river (Jones et al., 2008). The highest mean surface salinity was observed above the shelf (30.8 ± 0.9) and the Mendeleev Abyssal Plain (29.7 ± 1.3) with a maximum of 31.7 at 80° N (St. P80). The lowest salinities were found in the Canada Abyssal Plain (26.4 ± 1.5) and over the ice-free waters of the Chukchi Abyssal Plain (27.5 ± 1.7).

Euphotic depth. The euphotic zone was twice as deep in the deep basins (63 ± 13 m) than over the shelf (33 ± 11 m, Fig. 2c). While deep basins are oligotrophic and receive less suspended matter from rivers, higher turbidity over the shelf is due to sediment re-suspension and higher primary production (Emmerton et al., 2008). Euphotic depth data are not available for the HIB because ice thickness prevented the deployment of instruments and data acquisition from satellites. However, recently Sun Yun et al. (2011) reported that, in 90% ice-covered areas of the Canada Abyssal Plain, the euphotic zone in summer was as deep as in the ice-free waters.

Nitrate concentration. The average nitrate concentrations in the euphotic zone are the highest over the Chukchi shelf (5.5 ± 3.4 μM) and decrease by a factor of 4 in the Canada Abyssal Plain. They are relatively high in the Chukchi Borderland averaging 3.2 ± 1.0 μM (Fig. 2d).

3.2 Spatial distribution of phytoplankton communities

3.2.1 Chl-*a* and pigment biomass

Accessory pigment concentrations in Arctic waters increase linearly with chlorophyll-*a* ($r^2 = 0.87$, not shown). The chlorophyll-*a* represents on average 50% of the total accessory pigments. The highest phytoplankton biomass was found in the SCM (red

line, Fig. 2e and green line, Fig. 2f), at the depth of the nutricline (red line, Fig. 2f) coinciding with the base of the surface fresh layer (SFL) defined by the 31 isohaline (blue line, Fig. 2f). Shallow SCM above the shelf (20 ± 9 m) deepens (37 ± 11 m) over the Chukchi Borderland and even more in the Canada Abyssal Plain (56 ± 14 m). Algal biomass in the deep basin surface waters is 10 times lower than in shelf surface waters. It is 5 times lower in the deep basin SCM than in shelf SCM.

In the following sections, we discuss separately the shallow Chukchi shelf from the oligotrophic Canada deep basin waters, and distinguish the SCM communities developing in the nutricline apart from those from fresh and nutrient depleted well-lit surface waters.

3.2.2 Accessory pigments

Shelf waters. The mean pigment concentration in shelf waters is three times higher in the SCM than at the surface. Values range from 0.20 to 5.60 mg m^{-3} at the SCM ($2.59 \pm 2.28 \text{ mg m}^{-3}$, Fig. 3b), and from 0.36 to 3.50 mg m^{-3} at the surface ($0.99 \pm 0.64 \text{ mg m}^{-3}$, Fig. 3a). The high pigment variability highlights the “patchiness” of the phytoplankton distribution. However, pigment distributions are quite similar in surface and subsurface waters. Shelf waters are characterized by high fucoxanthin (Fuco), produced mainly by diatoms, both in surface and SCM waters. Other pigments such as prasinoxanthin (Prasino), chlorophyll-*b* (chl-*b*), diadinoxanthin (Diadino) and carotenoids (Caro) account for 3 to 5 % of the total pigments. The peridinin (Peri) primarily synthesized by dinoflagellates represents less than 2 % of the accessory pigments.

Lowest pigment waters of the west coast of Alaska (Stations C31, R05, C23) are low in Fuco (40 %) while pigments typical of small-size species, such as Pras (10 %), chl-*b* (10–30 %), neoxanthin (Neo ~ 5 %) and alloxanthin (Allo ~ 5 %) increase pie charts in Fig. 3a, b. Of note, the high SCM concentrations of 19'-hexanoyloxyfucoxanthine (19HF, 1.69 mg m^{-3}) at station R17 (40 m) suggesting prymnesiophyte blooming over the continental slope, North of Chukchi shelf.

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Deep basin waters. Pigment composition in deep basin waters is different from the shelf waters (Fig. 4). While over the Chukchi shelf pigment distributions are similar in surface and SCM waters, they show distinct communities with depth in deep basin waters (pie charts in Fig. 4a and b). Surface waters of the Canada Abyssal Plain have a low pigment content (Fig. 4a) but Fuco dominates ($62 \pm 20\%$) in the ice covered and ice free areas, whereas Diadino prevails (44 %) in the MIZ followed by 19HF (5–25 %), the third major pigment. Highest concentrations are found near Barrow Canyon (S21, S22 and S14), at station P38 above the Northwind Ridge, and in the HIB and MIZ of the Chukchi Borderland. These relatively “rich” surface waters, as compared to Canada Abyssal Plain, have in most cases a similar pigment composition in the SCM. The most abundant pigments are Fuco (25–30 %), chl-*b* (23 %), Pras (11 %), 19HF (10 %) and Neo (4 %). Other pigments, zeaxanthin (Zea), 19'-butanoyloxyfucoxanthin (19BF) and violaxanthin (Viola) are present in smaller proportions (<4 %). Surface water pigments in the ice-free Chukchi Abyssal Plain are as low as in the Canada Abyssal Plain.

In the SCM of the deep basins, the total pigment concentrations are up 6 times higher than in surface waters (Fig. 4a, b). The main accessory pigments are successively Fuco, chl-*b*, Prasino and 19HF. They account for 80 % of the total accessory pigments and suggest that communities are dominated by prasinophytes (chl-*b* + Pras = 40 %), while diatoms (Fuco = 25 %) and prymnesiophytes (19HF = 15 %) account for the remainder. Chl-*b* and Prasino are 30 % higher in the Chukchi Borderland than in the Canada Abyssal Plain, while Fuco is 30 % higher in the Canada Abyssal Plain than in the Chukchi Borderland. 19HF locally reaches high values and dominates the total pigments at two stations, B11 and N81. The 19BF, Neo and Diadino were detected at all stations but in concentrations 5 times lower than the four dominant pigments mentioned above. Peri and divinyl chlorophyll-*a* (DVchl*a*), produced by dinoflagellates and prochlorophytes, respectively, were absent from the deep basin waters.

3.2.3 Taxonomy

Shelf waters. Above the Chukchi shelf, average phytoplankton abundance and biomass were of the same order of magnitude in surface and SCM waters (Table 1 and Fig. 5), but phytoplanktonic communities differ. In surface waters, unidentified nanoplankton dominates the abundance (52 %) and biomass (60 %), except for the southern shelf where centric diatoms *Chaetoceros* spp. and *Thalassiosira* spp. and the prymnesiophyte *Phaeocystis pouchetii* prevail (Fig. 5a, b, c). In the SCM, diatoms and nanoplankton are found in similar abundances (40 %) but the diatom biomass is 56 % while nanoplankton accounts for 34 % (Fig. 5d, e). About 80 % of the nanoplankton was unidentified, the remaining being represented by *Phaeocystis pouchetii* (15 %) and cryptomonads. (5%). The most abundant diatoms in the SCM are centric *Chaetoceros* spp. and *Thalassiosira* spp. in the southern shelf waters, while the northern shelf waters are dominated by pennate species *Fragilaria* sp. and *Fragilariopsis* sp. and centric diatom *Chaetoceros* spp. (Fig. 5f). It should be noted that, in the central shelf biomass is the lowest and is dominated by the dinoflagellate *Gymnodinium* sp. and the pennate diatom *Cylindrotheca* sp. Picoplankton (<2 μ m) accounts for <1 % of the total carbon biomass over the shelf and for 36 % and 16 % of total abundance in the surface and SCM waters, respectively.

In the deep basins, the total phytoplankton abundances are slightly higher in the SCM (930 ± 700 cells ml⁻¹) than in the surface waters (640 ± 510 cells ml⁻¹) (Table 1, Fig. 6a, d), but biomasses are similar. They are both 4 times lower than over the shelf. Highest values are found at two stations of the Chukchi Borderland (M01 and N01, Fig. 6). Surface and SCM phytoplankton abundances are dominated by picoplankton (55 %) and nanoplankton (40 %), while diatoms represent only 5 %. Compared to the shelf waters, diatom abundances are lower by a factor of 10, while nanoplankton abundances are 5 times lower. Picoplankton is 2 times less abundant in surface waters but increase at the SCM relative to the shelf. 95 % of the picoplankton could not be identified with the techniques we used. The few species identified are the prasinophyte

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Micromonas sp. consistently with Lovejoy et al. (2007). Much of the nanoplankton is not identified either (90%), however relatively high concentrations of the cryptophyte *Cryptomonas* sp. are found at station N01 and chrysophyte *Dinobryon belgica* over the Alpha Ridge.

5 The nanoplankton, abundant at all deep basin stations, accounts for 44% and 60% of the carbon biomass in surface and SCM waters, respectively. Nanoplankton largely dominates the low biomass waters (90%, $\sim 5 \text{ mgC m}^{-3}$) over the ice-free area of the basin. Although picoplankton is the most abundant phytoplankton compartment (55%) it accounts for only 5% of the total carbon biomass of the deep basin waters. Conversely, because of their large cell volume, the diatoms represent up to 70% of the total carbon biomass in surface rich areas of the MIZ and dominate the biomass in the SCM at ice-covered stations, north of 83° N (52%). The diatom species of the deep basins are different from those found over the Chukchi shelf. Of note the dominance of *Nitzschia* spp. in surface waters of the northern Chukchi Abyssal Plain (290 cells ml^{-1} , Fig. 6c, f). The remaining species consist of *Fragilariopsis* sp., *Actinocyclus* sp. in the Chukchi Borderland and *Minidiscus* sp. *Navicula* sp. and *Chaetoceros* sp., North of 84° N . Dinoflagellates *Gymnodinium* sp. and *Heterocapsa* sp. represent 35% of the SCM biomass in areas partially covered with ice over the MAP.

20 Our results show that while diatoms are present in minor abundances over the deep basins as compared to nanoplankton and picoplankton, they account for a major fraction of the total biomass. Conversely, the picoplankton represents half of the total cell number but a small proportion of the total biomass.

4 Discussion

4.1 Comparison between pigments and taxonomic counts

25 *Shelf waters dominated by fucoxanthin.* Both pigments and taxonomic data highlight the richness of the shelf waters in terms of cell abundance ($\sim 3000 \text{ cells ml}^{-1}$, Fig. 7a, b), carbon biomass ($\sim 100 \text{ mgC m}^{-3}$, Fig. 7c, d) and pigments ($\sim 2.5 \text{ mg m}^{-3}$, Fig. 7e, f). The phytoplankton abundance and biomass in shelf waters are on average 8 and

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4 times higher, respectively, than over the deep basins. Fuco suggests diatoms as dominant species of the phytoplankton population in surface and SCM waters of the Chukchi Shelf and taxonomy indicate *Chaetoceros* sp. *Cylindrotheca* sp. *Fragilaria* sp. and *Fragilariopsis* sp. *Thalassiosira* sp. as the main diatoms in SCM waters (Fig. 5f). These observations are consistent with previous taxonomic observations on the Chukchi shelf in 1994 (Booth et al., 1997) and 2003 (Seegreva et al., 2010). However, in surface waters our data reveal that 60 % of the carbon biomass over the shelf is nanoplankton (Fig. 7c) despite the large dominance of Fuco. Assignment of Fuco to diatoms by CHEMTAX may be responsible for this apparent discrepancy, as this pigment can also be a major pigment in prymnesiophytes (Jeffrey et al., 1997).

Picoplankton related pigments are very low over the shelf whereas this group represents 35% and 19% of the total cell number in surface and SCM, respectively. Picoplankton produces 100 and 1000 times less carbon than nanoplankton and microplankton, respectively, due to their low biovolume (Sun and Liu, 2003). As a result, pigment production is also much lower in picoplankton than larger cells. Pigments in shelf waters match biomass data better than abundance data.

Poor deep basin waters with poorly identified dominant species. The deep basin surface waters are oligotrophic and strongly dominated by diatoms (diadino + fuco) according to pigment data, while taxonomy determinations suggest dominant nanoplankton (Fig. 7a, c, e). However, under low total pigment concentrations, such as those of the surface of the Canada Abyssal Plain only pigments above the limit of detection, estimated to be here 0.05 mg m^{-3} , can be quantified. The detection of minor pigments by HPLC thus represents a limitation of the method that must be bare in mind. The taxonomic data of Segreeva et al. (2010) suggest a detection limit of phytoplankton species dominance for abundances of less than 50 cells ml^{-1} . In the southern and northern deep basins, microplankton cell concentrations are thus too low to infer dominant groups ($<10 \text{ cells ml}^{-1}$). Moreover, as for shelf waters we suspect that a large fraction of the Fuco is associated to other species such as prymnesiophytes or dinoflagellates, rather than diatoms (Rodriguez et al., 2002).

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The SCM cell abundances and carbon biomass were comparable to surface values but pigment biomasses are 5 times higher in the SCM. This finding likely reflects an increase of the cell pigment content in response to adaptation to low light availability at the SCM (Henriksen et al., 2002). Picoplankton and nanoplankton accounting for 55 % and 40 % of the cell abundances, respectively, and dominate in the SCM waters (Fig. 7b). Pigments indicate 53 % picoplankton and 35 % nanoplankton thus agreeing with cell abundances (Fig. 7f). CHEMTAX identifies picoplankton as prasinophytes and nanoplankton as chrysophytes (75 %) and prymnesiophytes (25 %) (Fig. 7f). Although pigments are good indicators of the dominance in phytoplankton cell numbers, they do not match the phytoplankton dominance in terms of carbon biomass in the deep basins. For example, pigment data suggest the presence of diatoms and minor nanoplankton at the SCM of the IFB, while the carbon biomass data indicate prevalent nano-size phytoplankton. Also, in the northern basin, the SCM water biomass is dominated by diatoms (56 %) while Fuco represents only 20 % and CHEMTAX results point to pico- and nano-plankton rather than diatoms.

“Hots spots” occurred in oligotrophic surface waters of the deep basin. Taxonomy and pigment data both show a significant high surface biomass and cell abundance in the MIZ. However, pigments in the MIZ indicate dominant prasinophytes, chrysophytes and diatoms while taxonomy suggests abundant unidentified picoplankton and nanoplankton and pennate diatoms (*Fragilariopsis* sp. *Nitzchia* spp.); biomass data points to unidentified nanoplankton. Only, at some stations, they both indicate dominant nanoplankton possibly because of monospecific “blooms”, as for example the high 19HF from prymnesiophytes at station N81 (72 %, Fig. 4b), or high biomass (28 mgC m⁻³) due to high cryptophytes (*Cryptomonas* sp. at station N01), as revealed by taxonomy (79.5° N, Fig. 6e).

Overall, pigments provide consistent information in the deep basin waters where cell abundances are dominated by small phytoplankton, largely unidentified (75 %). Pigments seem to reflect phytoplankton cell number in oligotrophic waters of the deep basins (chl-*a* = 0.1–1 mg m⁻³) while they are better linked to phytoplankton biomass

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in the eutrophic areas such as the Chukchi Shelf waters ($\text{chl-}a > 1 \text{ mg m}^{-3}$). In the oligotrophic surface waters of the deep basins ($< 0.05 \text{ mg chl-}a \text{ m}^{-3}$), CHEMTAX may be misleading because of the low ratio of accessory pigments relative to chl-*a*. We suggest that in the deep basin and shelf waters much of the Fuco is produced by nanoplankton rather than to diatoms. Cross-comparison of pigments and taxonomic data thus provide a more accurate approach to more accurately diagnose phytoplankton populations. Improvement of our understanding of the relationship between taxonomic enumeration and pigment fingerprints would benefit from additional field data.

4.2 Comparison with previous expeditions in the Canadian Arctic

Phytoplankton distributions in the Pacific sector of the Arctic Ocean under reduced ice cover such as those encountered in summer 2008 are limited. The only data available for comparison to the CHINARE 2008 cruise area are those of the Arctic Ocean Section (AOS) in summer 1994 and from the Shelf-Basin Interactions program (SBI), in summer 2002. We first compare our pigment data with those obtained in summer 2002 from the Chukchi shelf and the southern Canada Abyssal Plain (Hill et al., 2005). We then compare our taxonomic data to those acquired in August 1994 in the Chukchi Borderland and the Mendeleev Abyssal Plain (Booth et al., 1997). The lower ice cover in summer 2008 as compared to summers 1994 and 2002 allows us to explore the effect of ice retreat and freshwater input on the phytoplankton community (Fig. 9).

4.2.1 Comparison of the phytoplankton distributions in 2008 and 2002 over the Chukchi shelf and slope

The average chlorophyll-*a* concentrations North of Chukchi shelf in summer 2008 ($2.3 \pm 1.6 \text{ mg chl-}a \text{ m}^{-3}$) are similar to those found in summer 2002 ($2.0 \text{ mg chl-}a \text{ m}^{-3}$, Hill and Cota, 2005). Nevertheless, Hill et al. (2005) reported the occurrence of phytoplanktonic blooms at the shelf-break and thus locally high biomass ($40 \text{ mg chl-}a \text{ m}^{-3}$) and high production rate (8 mg C h^{-1}). Such bloom conditions are not observed in 2008,

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where chlorophyll-*a* concentrations never exceed 1.4 mg m^{-3} (St. S24, Fig. 4b). Fuco over the Chukchi Shelf was 3 times larger in 2008 than 2002. We found more diatoms in 2008 than in 2002, when pigment distributions underline prevailing small phytoplankton like prasinophytes (chl-*b*, Pras). In the SCM, in both years, the phytoplankton communities are dominated by more than 80 % by large phytoplankton. However, in 2008 accessory pigments are 75 % Fuco, while in 2002 Fuco amounts 49 % and chlorophyll c1 and c2, 21 %, but the two latter are commonly found in large phytoplankton.

Over the slope and the deep Canada Abyssal Plain, chlorophyll-*a* concentrations in 2008 indicate oligotrophic conditions in surface waters with values $<0.1 \text{ mg chl-}a \text{ m}^{-3}$ and around $0.2 \text{ mg chl-}a \text{ m}^{-3}$ at the SCM, as also found in 2002 ($<0.5 \text{ mg chl-}a \text{ m}^{-3}$, Hill and Cota, 2005). In 2008, pigments from chrysophytes and prymnesiophytes (19HF, 19BF) represent 25 % of total pigment at the SCM, while these two groups were minor in 2002. In contrast, Fuco was higher in 2002, suggesting that nanoplankton dominated over diatoms in 2008. The relative proportions of picoplankton pigments, Pras and chl-*b*, are of the same order of magnitude. In surface deep basin waters, pigments associated to large phytoplankton is higher in 2008, those produced by small species decrease drastically. Indeed, the chl-*b* and Pras are 3 and 5 times lower in 2008 than in 2002; the 19HF are threefold higher in 2008, and Fuco rises from 16 % to 45 %.

Overall, pigment data highlight larger phytoplankton communities in shelf waters in 2008 than 2002, and a larger proportion of nanoplankton in the deep basin waters in 2008, at the expense of picoplankton in surface waters, and at the expense of diatoms in the SCM.

4.2.2 Comparison of the phytoplankton distributions over the deep basins at high (1994) and low (2008) ice cover

The abundance and biomass of major phytoplankton groups measured during the CHINARE 2008 cruise are compared to those of the AOS transect (Gosselin et al., 1997) sampled in July–August 1994 in the same area. Both transects are similar over

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the Chukchi Borderland but differ North of 80° N. Sampling in 1994 was performed West of Mendeleev Abyssal Plain (~175° W longitude), while samples were taken East of the Mendeleev Abyssal Plain during CHINARE cruise.

Higher phytoplankton biomass in 2008 despite a drastic reduction in cell abundances. The most surprising observation is the lower abundance and biomass of picoplankton by a factor of 10 in 2008 (~450 cells ml⁻¹, Fig. 8a, b) as compared to 1994 (Fig. 8i, j) (~4500 cells ml⁻¹, Fig. 8g, h) at all stations and depths. In 1994, picoplankton accounts for 96 % of the total abundance and 20 % of the total biomass, but only 42 % of the abundance and 5 % of the total biomass, in 2008 (Fig. 8c, d). While, the total cell abundances is lower in 2008, the phytoplankton biomasses is higher by 20 % in surface waters and by 100 % at the SCM, most probably because of increased size of phytoplankton under reduced ice conditions. In particular, in 2008 the abundance of nanoplankton increases by 50 % at the surface and by threefold at the SCM. The concentrations of diatoms are similar for the two years, however in 1994, diatoms were dominated by “sub-ice species” *Melosira arctica*, while in 2008 “pelagic species” *Nitzschia* sp., *Fragilariopsis* sp., *Navicula* sp. and *Actinocyclus* sp. predominated. The dinoflagellate *Gymnodinium* sp., quite abundant in 1994 (~30 cell ml⁻¹) is lower by an order of magnitude in 2008 (Peri < 1 %). The increase in total biomass in 2008 is mainly due to increased abundance of nanoplankton identified as chrysophytes and prymnesiophytes by pigments analyses.

However, phytoplankton biomass and composition are not uniform and show differences in the MIZ (77–80° N), IFB (74–77° N) and HIB (80–86° N) in 2008 as compared to the same area in 1994 which was entirely ice covered, as discussed below.

Offshore “ice edge hot spots” and the proliferation of large phytoplankton in the MIZ. Biomass in the MIZ of the deep basins waters is higher in 2008 both in the surface (40.3 mgC m⁻³ in 2008 against 12.8 mgC m⁻³ in 1994) and SCM waters (29.1 mgC m⁻³ in 2008 against 9.0 mgC m⁻³ in 1994) as compared to the ice covered 1994. In surface waters, higher biomass is linked to diatoms *Nitzschia* sp. *Fragilariopsis* sp. and *Actinocyclus* sp. and unidentified nanoplankton which are 10 and 5 times higher, in

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2008. The cryptophytes, rare in 1994 ($<5 \text{ cells ml}^{-1}$), are also much higher in 2008 (79 cells ml^{-1}).

Impoverishment of the ice-free basins (IFB) where nanoplankton dominate. In 2008, lowest biomass (4.5 mgC m^{-3}) is associated with 10 and 20 times lower abundances of diatoms and dinoflagellates, respectively. Both surface and SCM waters contain more than 90 % nanoflagellates. In 1994, the biomass is 2–3 times higher and phytoplankton mainly composed of diatoms (45 %), large flagellates $>2 \mu\text{m}$ (30 %) and picoplankton (25 %).

Ice-covered areas (HIB) depleted in surface microplankton and enriched in SCM nanoplankton. In 2008, the biomass in surface waters North of 83°N is reduced compared to 1994: the diatom biomass is low in 2008 (1.2 mgC m^{-3}) and higher in 1994 (5.5 mgC m^{-3}), while the nanoflagellate biomass is similar. In the SCM, the nanoplankton biomass is 5 times higher in 2008 than in 1994.

4.3 Impact of ice melting on the phytoplankton distribution

The comparison between phytoplankton populations in 2008 and 1994 has shown that strong ice melting in 2008 promoted nanoplankton growth in Pacific sector of the Arctic Ocean, while the picoplankton and microplankton (dinoflagellates) declined. However, the response to melting is contrasted with evidences of “hots spots” of diatoms in the MIZ while this biomass decreases in the IFB. In the HIB, higher abundance and biomass are found at greater depth. Pigment data in 2002 and 2008 in southern Canada Abyssal Plain confirm these findings.

Major physical changes linked with the ice melting. The reduction of the ice cover and subsequent freshening of the upper water column are two key parameters for light and nutrient availability affecting photosynthesis, production rates and phytoplankton composition (Fig. 9). In 1994, all stations North of 75°N were sampled under thick ice cover ($>90\%$) (Fig. 9a). In 2008, the ice retreat above the deep basins led to three areas, the IFB, the MIZ and the HIB North of 80°N , yet even in the HIB, ice concentration always remains below the 1994 conditions (ice $>90\%$).

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The freshening depletes Arctic surface waters in nutrients and deepens the nutricline and SCM. Surface salinity in 2008 is lower by 2 to 6 units in the IFB and HIB than in icy year 1994 (Fig. 9b). Salinity in the MIZ at 10 m is similar in 1994 and 2008. Freshening of the deep basin reveals regional disparities due to variable influence of the river discharge and ice melting on surface salinity (McClland et al., 2006). One important consequence of freshening due to ice melting is the nutrient depletion of surface waters as a result of vertical stratification preventing supply of deep-water nutrients to the surface. Another major consequence of freshening is the formation of a thick SFL which causes a deepening of the nutricline and therefore of the SCM (Fig. 9d) (McLaughlin et al., 2010). Our data show that the southern and northern deep basins are more strongly affected by freshening in 2008, with surface nutrient concentrations five times lower ($0.40 \pm 0.25 \mu\text{M}$) than in 1994 ($1.97 \pm 0.63 \mu\text{M}$) (Fig. 9e). The SCM is 3 times deeper in 2008 ($42 \pm 10 \text{ m}$) than in 1994 ($14 \pm 8 \text{ m}$) (Fig. 9d). However, in the MIZ where the freshening is less pronounced the SCM shallows ($31 \pm 10 \text{ m}$) and the mean nitrate concentration in upper 25 m is 3 times higher in 2008 ($1.67 \pm 0.98 \mu\text{M}$) than in 1994 ($0.65 \pm 0.33 \mu\text{M}$). Even though vertical stratification resulting from freshening affects surface nutrient concentrations, consumption by phytoplankton must be considered. Notably, the high nitrate concentrations in the MIZ likely sustain early diatom and nanoplankton bloomings in the process of ice melting (Fig. 9g, h).

The effect of solar irradiance in the surface layer (~100 m) in ice-free conditions is another important factor influencing the phytoplankton distribution. Data obtained in summer 2009 in the Canada Basin show that ice-covered areas (>90%) have a euphotic depth similar to the ice-free part of the basin (ice = 0%) (Sun Yun et al., 2011). Over the recent summers, the thinning of ice and removing of snow over the ice in deep basins favored light penetration across the ice. Thus, rather than the direct effect of light, freshening by deepening the nutricline would exert control on biomass, abundance and diversity of phytoplankton during summer. The SFL thickness would thus drive the nutricline and thus phytoplankton growth depth: deeper nutricline sustains deeper but less productive phytoplankton communities due to light attenuation.

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Conversely, photo-inhibition in near surface nutricline waters also affects phytoplankton (Finkel et al., 2010). Picoplankton sensitivity to high irradiance and UV exposure may explain the low prasinophytes in surface waters under extended ice retreat in 2008 as compared to 1994 (Key et al., 2010). In the HIB during 2008, higher freshening led to a SFL at about 40 m, with a decrease of large phytoplankton in surface waters (diatoms and dinoflagellates) and maximum phytoplankton biomass and abundances at greater depth. In contrast, freshening in 1994 was reduced and phytoplankton mainly grew in surface waters.

An “offshore ice edge bloom” in the MIZ. Increase abundances of diatoms and nanoplankton in 2008 in the MIZ (77–80° N) led to the formation of “off-shore ice-edge blooms” as also found in marginal Arctic seas (Alexander and Niebauer, 1981; Luchetta et al., 2000; Hill et al., 2005; Tremblay et al., 2006; Sukhanova et al., 2009). The recent withdrawal of ice in the MIZ, increase solar irradiance together with a shallow nutricline likely provide optimal conditions for large cell growth. The highest biomass in “offshore ice edge blooms” (M01, N01, Fig. 6b, e) is of the same order of magnitude as the mean biomass value over the shelf and 3 times lower than at the ice-edge of the Chukchi Shelf (R11, R13, Fig. 5e). Species in “offshore ice edge blooms” are also different from those living in ice edge over the shelf. The ice-edge over the shelf is dominated by diatoms like *Chaetoceros* spp. *Fragilaria* sp. and *Fragilariopsis* sp. and unidentified nanoplankton or *Phaeocystis pouchetii* while “offshore ice edge blooms” are composed of pennate diatoms *Nitzschia* sp. and *Fragilariopsis* sp., and nanoplankton like dictyochophytes or crysophytes. It is important to emphasize that in ice edge waters over the Canada Abyssal Plain pigment biomass does not significantly increase, neither in surface nor at SCM waters, unlike in the MIZ of the Chukchi Borderland. We can speculate that nutrient replenishment from upwelled deep waters is favored under thin MIZ rather than thicker Canadian basin SFLs.

The strong stratification due to intense freshening drives the ice-free zone (IFB) to oligotrophy. In the IFB freshening induces nutrient depletion of surface waters and the deepening of the SCM to about 40–50 m. As a result, microplankton and picoplankton

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declined in surface waters as compared to 1994 and remain low even in the SCM. The nanoplankton does not show significant changes between 2008 and 1994, seemingly because of better adaptation to ice retreat.

5 Conclusions

During the IPY (2007–2008), a major effort was undertaken to acquire hydrological data in Polar regions, among which the Arctic Ocean, where phytoplankton and nutrient data are scarce. Samples from the CHINARE 2008 cruise provide new pigment and taxonomy data in a poorly documented area of the deep central basin of the Arctic, after the extreme ice melting conditions of summer 2007.

The phytoplankton composition in the Pacific Arctic Ocean reveals important changes as a result of recent ice shrinking over the deep basins. In 2008, we find dominant nano-sized chrysophytes in the deep basins and a decline of pico-sized prasino-phytes and micro-sized dinoflagellates. The diatoms are found in lower abundances in the ice-free (ice < 20 %) and heavy ice (ice > 70 %) waters of the deep basins, but elevated values in the marginal ice zone (20 % < ice < 70 %). High Fuco over the shelf and in the surface waters of the deep basins suggest that besides diatoms, nanoflagellates likely produce this pigment.

The retreat of ice over the deep basins led to regional contrasts in phytoplankton size and abundances. At high latitudes, in partially ice covered deep basins (ice ~70%), the phytoplankton biomass is low in surface waters due to diminished abundances of large species, rising in the SCM. A shift from ice diatoms to deeper pelagic community dominated by nano-sized phytoplankton accompanies the ice cover reduction. In the marginal ice zone of basins (77–80° N), localized “hot spots” with high abundances of large phytoplankton occur as already reported in Arctic shelf ice-edges.

Earlier studies suggested that increase light availability due to ice retreat would result in increased PP and biomass. We propose that freshening, by deepening the nutricline and the SCM would reduce light available for phytoplankton growth. Likewise, stronger

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stratification would constrain nutrients availability for surface communities. Lower nutrients and light availability would promote nanoflagellates (chrysophytes, prymnesiophytes) growth in surface waters, while picoplankton, less adapted to higher and longer exposure to UV, declines in surface waters.

5 Our data evidence differences in the phytoplankton structure (cell size, species and abundances) in deep basin surface waters between heavily ice-covered (summer 1994) and ice-free or partially ice-covered years (summer 2008), yet phytoplankton biomass is similar. While we document impoverishment of ice-free basins, we see enrichment at offshore ice edges. Nevertheless, with the northern extension of the ice-free areas
10 and enhanced freshening subsequent to predicted increase of ice melting and river discharges, impoverishment of the ice-free basins would extend northward. The deep Arctic basins would thus evolve towards decreasing phytoplankton biomass and production. We can thus anticipate that carbon production and export would decrease in the ice-free basins and increase in the marginal ice zone, as a consequence of
15 changes in the phytoplankton abundance and size structure.

Future CHINARE cruises planned every other year in the Arctic should provide additional biogeochemical data to improve our understanding of the response of phytoplankton, from shelf to the deep basins, to on-going sea ice cover changes to ultimately produce a more comprehensive picture of the Arctic ecosystem evolution.

20 **Supplementary material related to this article is available online at:**
**[http://www.biogeosciences-discuss.net/9/2055/2012/
bgd-9-2055-2012-supplement.pdf](http://www.biogeosciences-discuss.net/9/2055/2012/bgd-9-2055-2012-supplement.pdf)**

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Table 1. Average abundances, carbon biomass and relative contributions derived from CHEMTAX for 4 phytoplankton groups in surface and SCM waters.

SURFACE	Diatoms (20–200 µm)	Dinoflagellates (10–100 µm)	Nanoplankton (2–20 µm)	Picoplankton (<2 µm)	Total
Abundance (cell ml ⁻¹)					
SHELF (68–74)	362.0 (12.2)	0.2 (0.0)	1542.8 (51.9)	1068.6 (35.9)	2973.6
BASINS (68–86)	32.9	2.0	245.9	390.5	671.3
IFB (75–77)	11.3 (4.1)	0.0 (0.0)	139.4 (50.0)	128.0 (45.9)	278.7
MIZ (78–82)	92.2 (8.7)	4.6 (0.4)	396.8 (37.3)	569.1 (53.6)	1062.6
HIB (83–86)	12.3 (2.9)	0.2 (0.0)	148.8 (35.0)	263.4 (62.0)	424.6
Carbon biomass (mgC m ⁻³)					
SHELF (68–74)	29.4 (37.8)	0.4 (0.5)	47.2 (60.7)	0.7 (0.8)	77.7
BASINS (68–86)	5.6	1.8	7.7	1.3	16.4
IFB (75–77)	0.4 (8.8)	0.0 (0.0)	4.0 (90.3)	0.0 (0.6)	4.4
MIZ (78–82)	14.4 (45.0)	3.0 (9.3)	12.6 (39.5)	2.0 (6.3)	32.0
HIB (83–86)	0.8 (13.9)	0.7 (11.5)	4.1 (66.8)	0.5 (7.6)	6.1
CHEMTAX (%)					chl-a
SHELF (68–74)	92.6	0.0	4.6	2.8	1.19
BASINS (68–86)	49.9	0.2	19.0	30.9	0.14
IFB (75–77)	58.0	0.3	19.5	22.3	0.10
MIZ (78–82)	17.2	0.1	27.8	54.9	0.21
HIB (83–86)	99.4	0.2	0.2	0.3	0.04
SCM					
Abundance (cell ml ⁻¹)					
SHELF (68–74)	959.4 (40.6)	11.2 (0.5)	1009.6 (42.7)	385.5 (16.3)	2365.6
BASINS (68–86)	31.6	3.6	377.2	561.5	974.0
IFB (75–77)	0.4 (0.1)	0.0 (0.0)	160.4 (41.4)	226.8 (58.5)	387.6
MIZ (78–82)	22.9 (2.1)	3.3 (0.3)	556.8 (52.2)	484.4 (45.4)	1067.4
HIB (83–86)	72.7 (5.8)	6.7 (0.5)	240.1 (19.2)	929.1 (74.4)	1248.7
Carbon biomass (mgC m ⁻³)					
SHELF (68–74)	55.8 (55.6)	10.2 (10.2)	34.3 (34.2)	0.1 (0.1)	100.4
BASINS (68–86)	4.5	2.7	13.3	0.6	21.1
IFB (75–77)	0.1 (1.6)	0.0 (0.0)	4.7 (97.3)	0.0 (1.0)	4.9
MIZ (78–82)	3.7 (14.0)	2.9 (11.1)	19.7 (74.5)	0.1 (0.4)	26.4
HIB (83–86)	9.1 (38.5)	4.2 (17.6)	8.2 (34.5)	2.2 (9.3)	23.6
CHEMTAX (%)					chl-a
SHELF (68–74)	88.1	0.2	4.9	6.8	2.16
BASINS (68–86)	10.8	0.7	35.1	53.4	0.50
IFB (75–77)	15.9	0.9	32.1	51.1	0.69
MIZ (78–82)	9.3	0.8	43.2	46.7	0.40
HIB (83–86)	2.5	0.0	23.4	74.1	0.28

The % abundance and carbon biomass are given in parenthesis. Stations where taxonomic data are available were grouped according to bathymetry as Shelf and Basins. Basins are subdivided according to ice conditions: ice-free basins (IFB), marginal ice zone (MIZ) and the heavy ice basins (HIB).

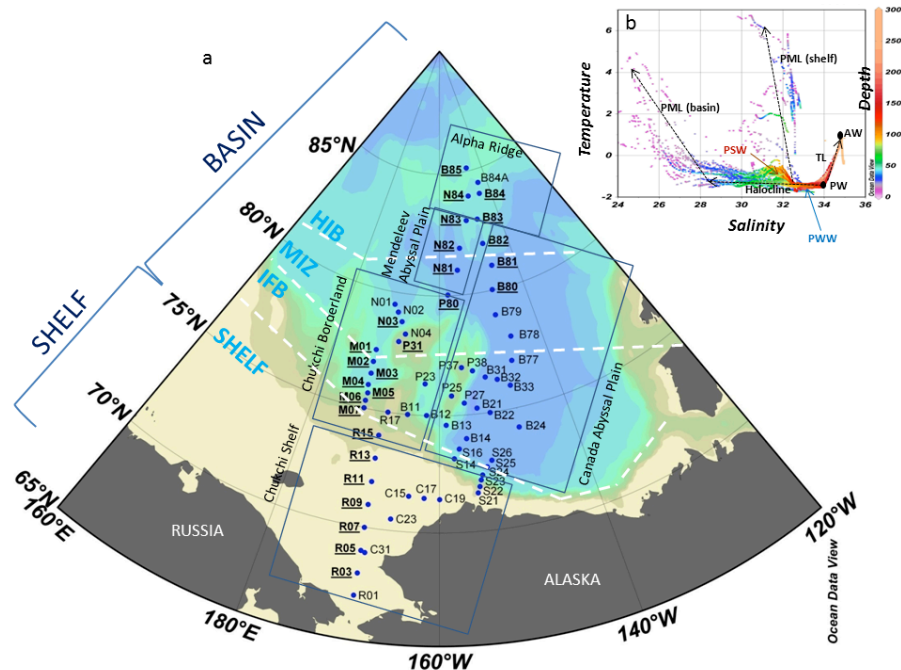


Fig. 1. (a) Sampling stations during the CHINARE 2008 cruise performed on-board of the “Xue-Long” icebreaker (1 August–8 September 2008). Blue dots are pigment stations. Bold and underlined indicate the stations where taxonomy data are available. Four areas are distinguished based on the bathymetry and ice concentrations: the shelf, the ice-free basins IFB (ice < 20%), the marginal ice zone MIZ (20% < ice < 70%) and the heavy-ice basin HIB (ice < 70%) including the Mendeleev Abyssal Plain, MAP, **(b)** temperature vs. salinity diagram plotted from the CTD data during CHINARE 2008. Polar Mixed layer (PML), thermocline layer (TL), Atlantic Water (AW), Pacific Water (PW), Pacific Summer water (PSW) and Pacific Winter Water (PWW).

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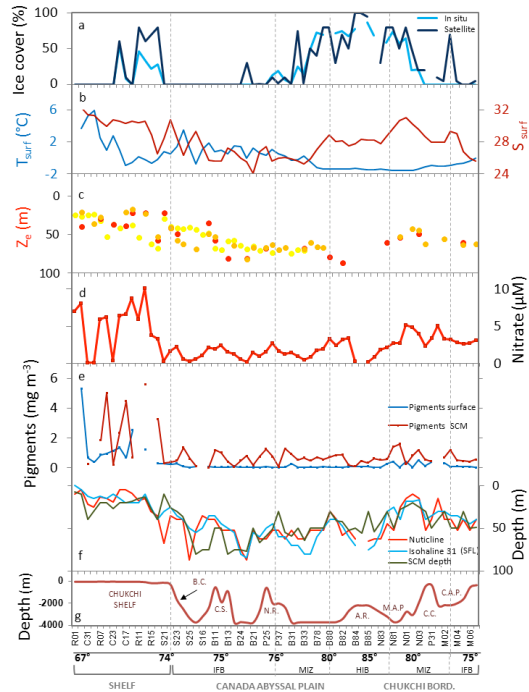


Fig. 2. Physical and environmental parameters over the Chukchi Shelf, the Canada Abyssal Plain and the Chukchi Borderland. IFB, MIZ and HIB are defined in Fig. 1 caption. **(a)** Ice concentration (in %) from in situ data (light blue line) and Special Sensor Microwave Imager (SSM/I) daily satellite data (level 2 products at 12.5 km spatial resolution) (in dark blue line); **(b)** sea surface temperature and surface salinity from conductivity-temperature-depth (CTD) system (Sea-Bird SBE 9); **(c)** euphotic depth (in m) calculated by MODIS satellite (yellow dots) and by two methods based on in-situ CTD data (Zhao et al., 2010) (red dots) and based on 1 % light depth determined with a Secchi disk (orange dots); **(d)** nitrate concentration averaged over the euphotic layer (in μM); **(e)** concentration of total pigments in surface and Subsurface Chlorophyll Maximum (SCM); **(f)** depth of the nutricline (in m), depth of the SCM and depth of the Surface Fresh Layer (SFL) determined by the position of the isohaline 31 (in m), **(g)** main topographic features: Barrow Canyon (BC), Continental Slope (CS), Northwind Ridge (NR), Alpha Ridge (AR), Mendeleev Abyssal Plain (MAP), Chukchi Cap (CC) and Chukchi Abyssal Plain (CAP).

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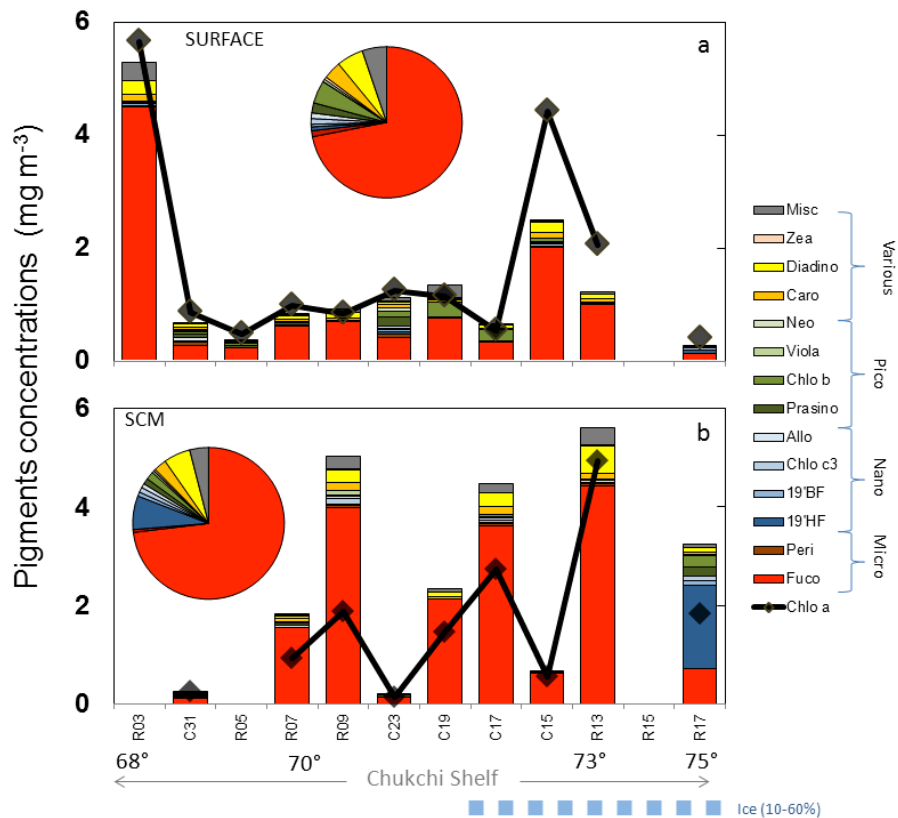


Fig. 3. Concentrations of chlorophyll-a (chl-a) and major accessory phytoplankton pigment (in mg m^{-3}) (see supplementary Table 1 for pigment acronyms) over the Chukchi Shelf in **(a)** surface waters and **(b)** in the SCM. The miscellaneous group (Misc) refers to pigments present in proportions $<2\%$, i.e. Chlc2, Diato, Lut, DVchla. The pie graphs show the mean relative proportions of the major accessory pigments.

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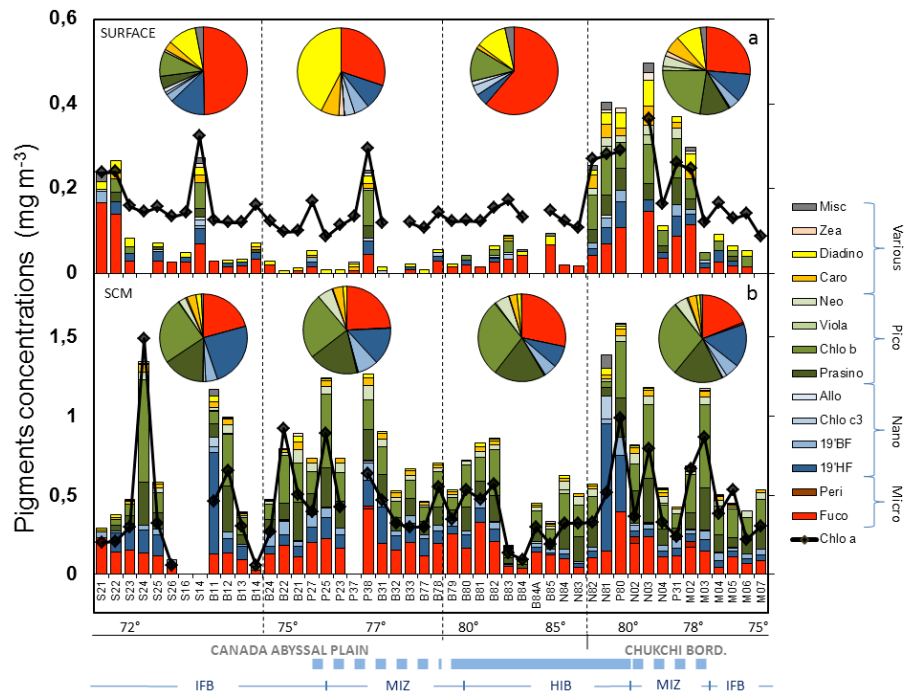


Fig. 4. Concentrations of chlorophyll-*a* (chl-*a*) and major accessory phytoplankton pigment concentrations (in mg m^{-3}) (see supplementary Table 1 for pigment acronyms) over the Chukchi Borderland and the Canada Abyssal Plain in **(a)** surface waters and in **(b)** the SCM. The miscellaneous group (Misc) refers to pigments present in proportions $<2\%$, i.e. Chlc2, Diato, Lut, DVchl_a. The pie graph shows the mean relative proportions of the major accessory pigments.

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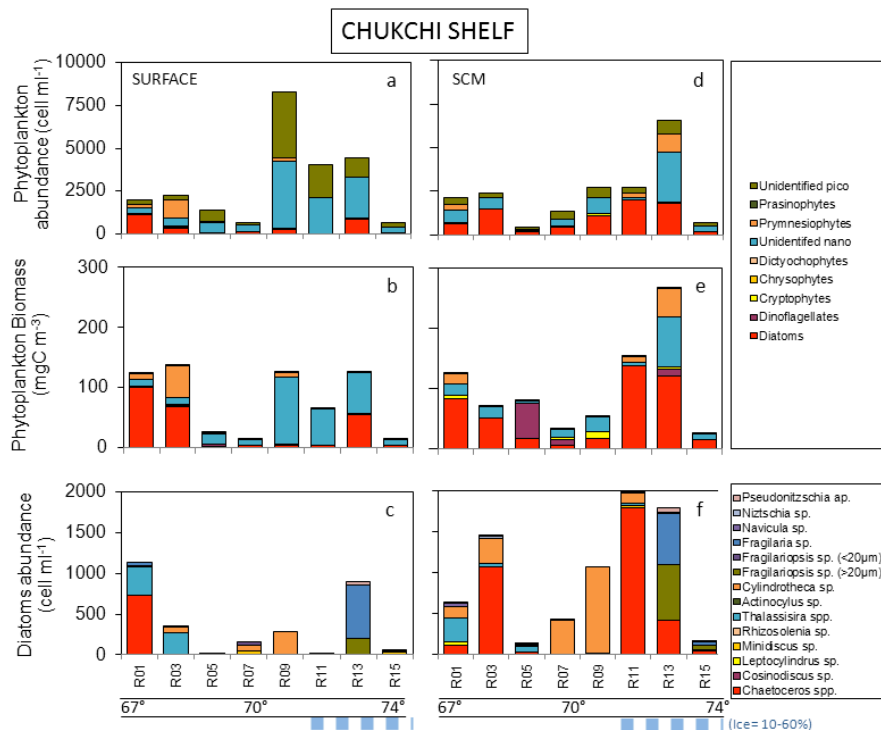


Fig. 5. Phytoplankton abundance and carbon biomass derived from microscopic counts in surface water (left panels) and in the SCM (right panels) over the Chukchi Shelf. The four upper panels show the abundance (**a-d**) and carbon biomass (**b-e**) of the major taxa. Two bottom panels (**c-f**) show the abundance of the 14 dominant species of centric and penate diatoms.

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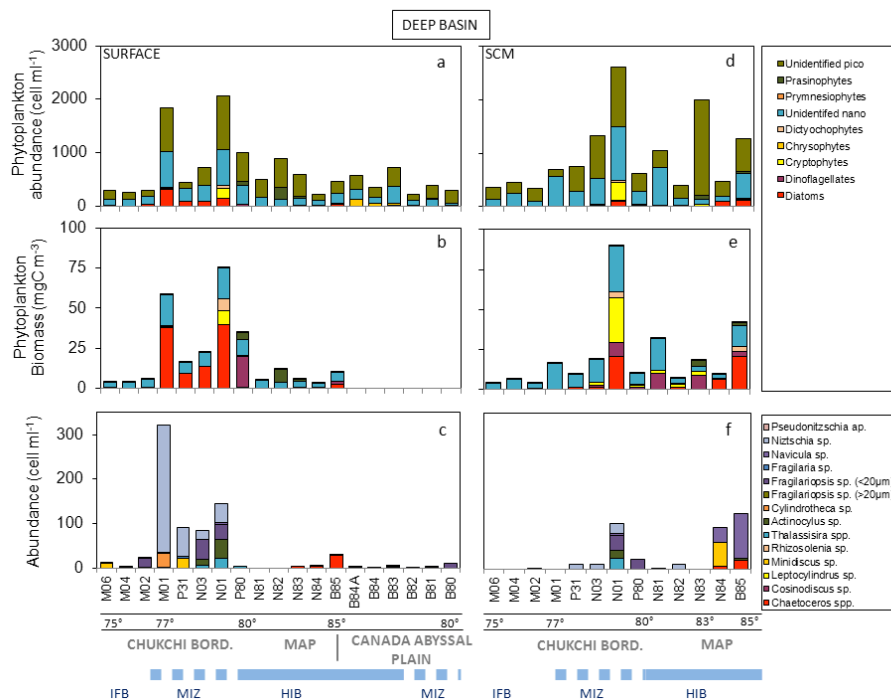


Fig. 6. Phytoplankton abundance and carbon biomass derived from microscopic counts in surface (left panels) and SCM (right panels) over the Chukchi Borderland, Mendeleev Abyssal Plain (MAP) and the Canada Abyssal Plain. The four upper panels show the abundance (**a–d**) and carbon biomass (**b–e**) of the major taxa. Two bottom panels (**c–f**) show the abundances of the 14 dominant species of centric and penate diatoms.

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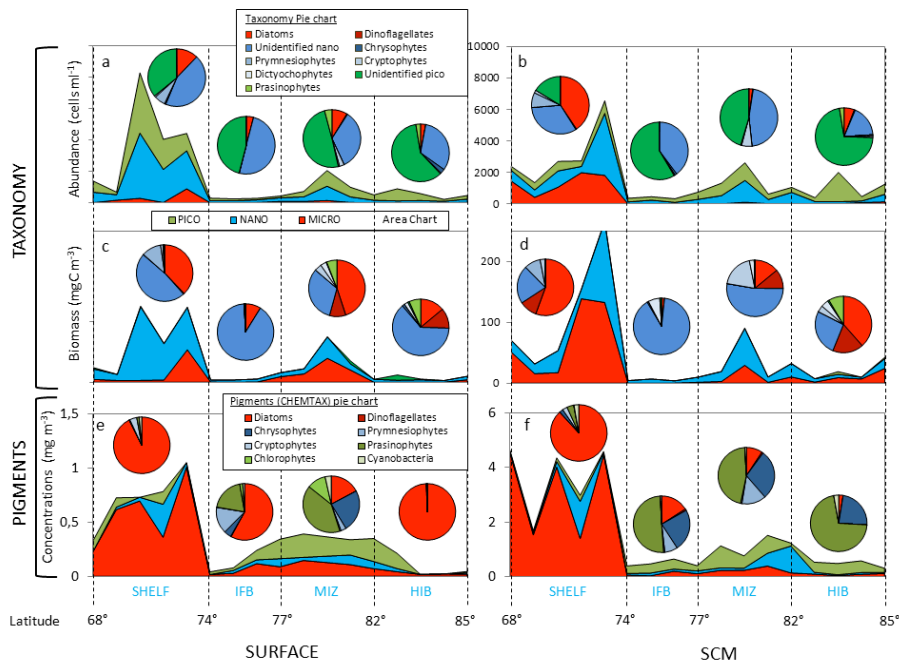


Fig. 7. Distribution of major groups of phytoplankton obtained by taxonomy (**a, b, c, d**) and pigments (**e-f**) in surface water (left panels) and in the SCM (right panels). Area charts show the abundance (**a, b**) and carbon biomass (**c-d**) of pico-, nano- and microplankton derived from taxonomy over the shelf, the ice-free basins (IFB), the marginal ice zone (MIZ) and heavy-ice basin (HIB). Area charts (**e, f**) show abundance of pico-, nano- and microplankton derived from pigment concentrations. Pie charts show (**a, b, c, d**) major phytoplankton groups derived from taxonomy counts. Pie charts show (**e, f**) the major phytoplankton groups calculated by the matrix factorization program CHEMTAX.

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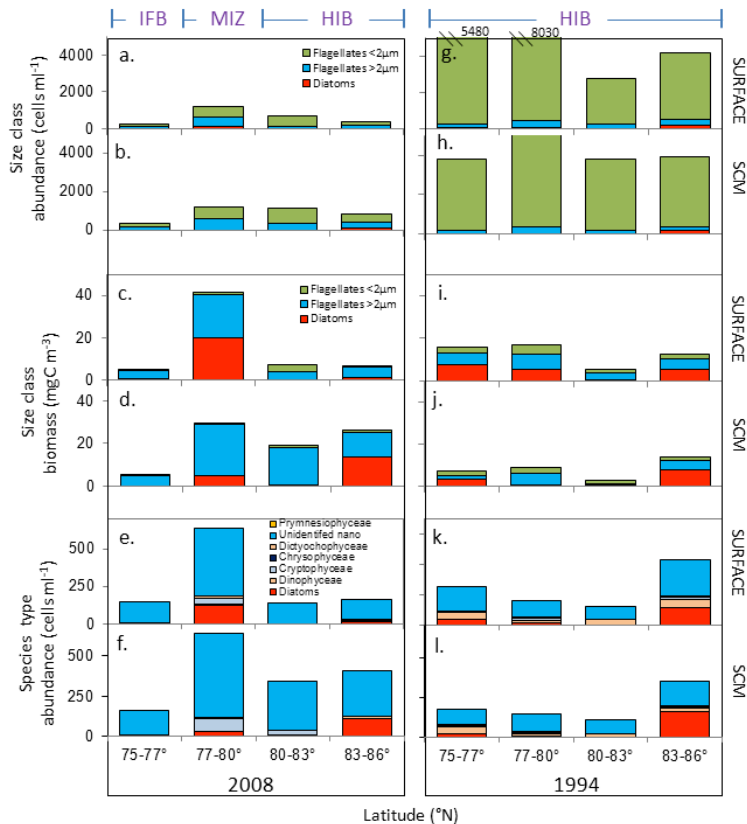


Fig. 8. Comparison of the taxonomic distribution of phytoplankton obtained during the CHINARE 2008 (left panels) and AOS 1994 (right panels) cruises. The phytoplankton abundances (**a, b, g, h**) and biomass (**c, d, i, j**) of three size classes: flagellates (<2 μM), flagellates (>2 μM) and diatoms in surface waters and in the SCM. (**e, f, k, l**) show the abundances of planktonic taxa.

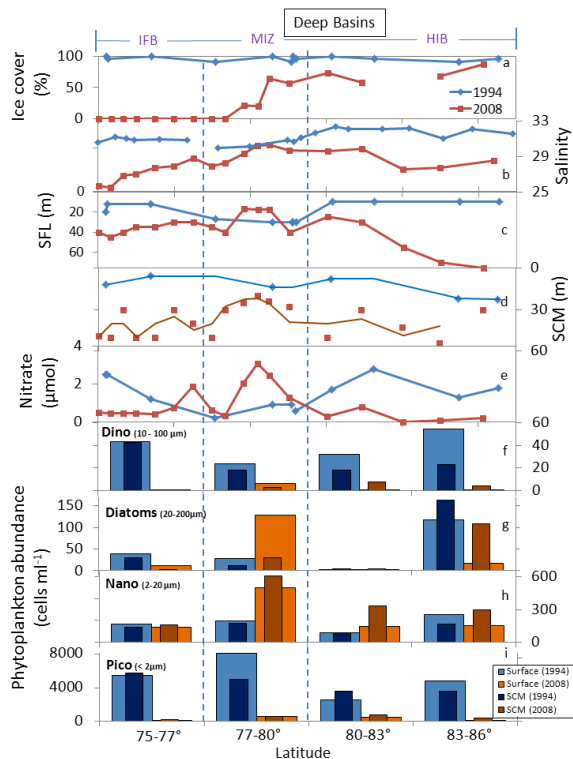


Fig. 9. Environmental parameters (five top panels) and mean phytoplankton abundances in surface waters and in the SCM during summer 1994 (blue bars) and 2008 (orange/brown bars) in the deep basins. Ice conditions are indicated on the top of the panels: IFB (ice-free basin), MIZ (marginal ice zone), HIB (heavy-ice basin). Ice cover (**a**), salinity at 10 m (**b**), SFL depth (**c**), SCM depth (**d**) and averaged nitrate concentrations in the upper 25 meters are presented for 1994 (blue lines) and 2008 (orange line) (**e**). Lower panels indicate cell abundances of dinoflagellates (**f**), diatoms (**g**), nanoplankton (**h**) and picoplankton (**i**) averaged for each zones.

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