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Characterizing the subsurface chlorophyll *a* maximum in the Chukchi Sea and Canada Basin

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ABSTRACT

Throughout the Arctic Ocean, subsurface chlorophyll a (Chl a) maxima (SCM) develop every summer after the water column stratifies and surface nutrients have been exhausted. Despite its ubiquity, the SCM's distribution, seasonal dynamics, and productivity remain uncertain. Here we present the first indepth analysis of the SCM in the Chukchi Sea and adjacent Canada Basin, drawing on data collected during the field program Impacts of Climate on the EcoSystems and Chemistry of the Arctic Pacific Environment (ICESCAPE). The SCM was significantly shallower on the Chukchi shelf (30 m) than in the Canada Basin (56 m), and in both regions was correlated with the euphotic and nitracline depths, suggesting an actively growing community maintaining its optimal position within the water column, consistent with previous work. The SCM was located significantly deeper than the net primary productivity (NPP) maximum, which averaged 15 m depth. The development of the SCM on the Chukchi shelf appears tightly linked to under-ice blooms, beginning ~ 1 month prior to sea-ice retreat and reaching \sim 15 m depth by the time ice retreats, beyond the range of satellite ocean-color sensors. A seasonal analysis of historical data from the region shows that the SCM deepens to \sim 30 m by July and remains there throughout the summer, a depth that is consistent with previous studies across the pan-Arctic shelves. We employed a spectral model of light propagation through the water column to demonstrate that surface Chl a and CDOM play approximately equal roles in attenuating light, limiting euphotic depth, and therefore SCM depth, to \sim 30 m, thus greatly limiting new production. If surface Chl a and CDOM were reduced, allowing greater light penetration, new production on Arctic shelves could potentially be 40% greater.

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1. Introduction

In the Arctic summer, after the water column stratifies and spring phytoplankton blooms have depleted inorganic nitrogen (N) in surface waters, a subsurface chlorophyll *a* (Chl *a*) maximum (SCM) commonly develops (e.g. Carmack et al., 2004; Martin et al., 2010). Dominated by large diatoms (such as *Chaetoceros* and *Thalassiosira*), this subsurface phytoplankton community is a pervasive feature of the Arctic marine environment throughout the summer and early fall. SCM have been observed on the continental shelves of the Chukchi (Cota et al., 1996; Codispoti et al., 2005), Beaufort (Carmack et al., 2004), Greenland (Cherkasheva et al., 2013), Barents (Kristiansen and Lund, 1989), Laptev (Heiskanen and Keck, 1996), and East Siberian seas

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http://dx.doi.org/10.1016/j.dsr2.2015.02.010 0967-0645/© 2015 Published by Elsevier Ltd. (Codispoti and Richards, 1971), as well as in the Canadian Arctic Archipelago (Martin et al., 2010; Booth et al., 2002), North Water Polynya (Klein et al., 2002) and Canada Basin (Lee and Whitledge, 2005; Nishino et al., 2008).

Despite its ubiquity, the ecological significance of the SCM remains uncertain for several reasons. First, it is unclear to what extent the SCM represents the sinking remains of a surface bloom versus an actively growing phytoplankton community maintaining its optimal position in the water column with respect to the opposing gradients of light (higher above) and nitrate (higher below). Several studies have noted a high fraction of diatom resting spores within the SCM, suggesting a moribund community (Heiskanen and Keck, 1996; Booth et al., 2002; Sukhanova et al., 2009). On the other hand, recent research points to active photosynthesis and new production within the SCM (Hill and Cota, 2005; Tremblay et al., 2008; Martin et al., 2010; Palmer et al., 2013).

Second, despite its ease of measurement, Chl *a* is an imperfect metric of phytoplankton abundance (Cullen, 1982). Because





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phytoplankton growing at low light may produce 5–10 times as much Chl *a* per cell as those growing at high light (Falkowski and Raven, 2007), the SCM may partially represent the effect of photoacclimation rather than a true maximum in phytoplankton biomass. For example, Lee and Whitledge (2005) observed that the ratio of Chl *a* to organic carbon in the Canada Basin was nearly 20 times higher at the SCM than at the surface.

Third, the productivity of the SCM remains in question. Because of the exponential decay of photosynthetically active radiation (PAR) within the water column, the SCM is consistently exposed to very low light levels, placing an upper threshold on maximum productivity regardless of the extent of shade-adaptation of Arctic phytoplankton species (e.g., Palmer et al., 2013). Thus, although Chl *a* concentrations may be very high at the SCM, primary productivity is not necessarily at its maximum level at that depth within the water column. For example, Cota et al. (1996) observed that productivity maxima in the north Chukchi Sea were significantly shallower than the depth of the SCM.

The question of SCM productivity is particularly relevant to recent pan-Arctic satellite-based studies, which have shown a significant increase in Arctic marine net primary production (NPP) coincident with sea ice decline (e.g. Arrigo et al., 2008). Because ocean color sensors only capture the first optical depth of the water column, they often miss the SCM and potentially significantly underestimate water column NPP (e.g. Uitz et al., 2006; Tremblay et al., 2008). For example, the recent study of Hill et al. (2013) reports that correcting for subsurface production doubles estimates of pan-Arctic NPP. On the other hand, in a separate analysis using the same dataset, Arrigo et al. (2011) showed that the error in satellite-derived NPP estimates associated with removing the SCM averages only 7.6%. They attribute this surprisingly small error to two main factors: (1) the largest errors occur when surface Chl *a* is low and the SCM is located very deep (>40 m), a situation that is rare in Arctic waters, and (2) satellite-based productivity algorithms do not assume negligible NPP at the depth of the SCM as is commonly believed, but rather calculate NPP at all depths using a parameterization of Chl a that does not include a SCM - therefore, satellite algorithms do not miss the entire NPP contribution of the SCM layer, but only a fraction thereof. Consistent with this, Ardyna et al. (2013) recently showed that vertical variations in Chl a have limited impact on annual depth-integrated Arctic Ocean NPP. Thus, although ubiquitous in nature and having been the subject of numerous studies in recent years, many important questions about the Arctic summer SCM (including its development (sinking vs. active growth), its biomass, and its contribution to Arctic primary production) remain unanswered.

The most comprehensive studies of the Arctic SCM to date were conducted in the Beaufort Sea and Canadian Arctic Archipelago (CAA) (Tremblay et al., 2008; Martin et al., 2010, 2012, 2013; Palmer et al., 2011; Ardyna et al., 2011; Ardyna et al., 2013). These studies clearly show that in these regions, phytoplankton within the SCM can rapidly acclimate to the attenuated light habitat of the subsurface (Tremblay et al., 2008; Palmer et al., 2011). The SCM maintains its vertical position near the nitracline (the depth at which nitrate (NO_3^-) concentrations rapidly increase to deep values), and therefore grows with a relatively high *f*-ratio (indicating substantial new production potentially available for export) compared to the surface community (Martin et al., 2012). Moreover, the SCM in these regions supplies a large fraction of the total annual new production (Martin et al., 2013). Thus, in the Beaufort Sea and CAA, the paradigm of the SCM as an actively growing, dynamic phytoplankton community that maintains its optimal water column position and contributes substantially to annual production has been well demonstrated (e.g. Martin et al., 2010).

In-depth studies of the SCM have yet to be undertaken in other regions of the Arctic Ocean, including the Chukchi Sea. The Beaufort Sea and CAA are very different from the Chukchi Sea due to their perennial freshwater stratification. Whereas the Beaufort Sea and CAA experience very limited surface nutrient renewal, even in winter, precluding intense surface spring blooms (hence the rapid development of the SCM in this region), the water column over the shallow Chukchi Sea shelf is thoroughly mixed at the start of the phytoplankton growing season, with surface NO₃⁻ concentrations of 10–15 μ mol L⁻¹ (Mills et al., 2015). This allows the Chukchi Sea to support the longest-lived surface bloom of any Arctic region (Arrigo and van Dijken, 2011). Furthermore, Arrigo et al. (2012) recently showed that these intense Chukchi Sea surface blooms can occur underneath the consolidated ice pack far from the ice edge. Similarly, Palmer et al. (2013) suggested that changing sea ice conditions may be resulting in a new pattern of seasonal productivity for the region. It is crucial to understand how these very different spring bloom dynamics affect the development of the SCM in the Chukchi Sea, and whether the emerging paradigm of an active, photosynthetically competent subsurface diatom community holds in this region as in the Beaufort Sea and CAA.

Here we present the first in-depth analysis of the distribution and seasonal dynamics of the SCM in the seasonally ice-free Chukchi Sea and Canada Basin. We draw on data from the recent NASA field program Impacts of Climate on the EcoSystems and Chemistry of the Arctic Pacific Environment (ICESCAPE), as well as historical cruise data from this region. Our goals are: (1) to map the distribution of the SCM and quantify its correlation to key physical and chemical variables of the Chukchi Sea and Canada Basin; (2) to assess the relationship of the SCM to NPP and export production; and (3) to use historical data to quantify and elucidate the seasonal development of the SCM.

2. Methods

2.1. Field sampling and analysis

We collected water samples for nutrients, dissolved gases, and particulate measurements on two cruises aboard the USCGC *Healy* to the Chukchi and Beaufort seas, HLY1001 (June 15–July 22, 2010) and HLY1101 (June 25–July 29, 2011), comprising the field portion of the NASA program ICESCAPE (Fig. 1).

At each station, water column profiles of temperature and salinity were measured using a conductivity-temperature-depth system (CTD; SBE 911 + Sea-Bird Electronics, Inc.) attached to a rosette. Additional instruments on the rosette included an oxygen (O_2) sensor (SBE43, Sea-Bird Electronics, Inc.), two transmissometers (C-Star red and blue, WET labs), a photosynthetically active radiation (PAR) sensor (QSP2300 PAR, Biospherical Instruments, Inc.), and a fluorometer (AQIII, Chelsea Technologies Group, Ltd.). In this study, we use only measurements made during the downcast. Seawater was collected into twelve 30 L Niskin bottles at discrete depths, typically the surface and bottom depths, as well as 10 m, 25 m, 50 m, 100 m, 150 m, and 200 m. When present, we also collected seawater from the depth of the fluorescence maximum.

2.2. Analytical methods

Concentrations of nitrate (NO₃⁻), nitrite (NO₂⁻), ammonium (NH₄⁺), silicate (Si(OH)₄), and phosphate (PO₄³⁻) in discrete water samples were analyzed on-board with a Seal Analytical continuous-flow AutoAnalyzer 3 (AA3) using standard methods (Armstrong et al., 1967; Bernhardt and Wilhelms, 1967; Kerouel and Aminot, 1997).



Fig. 1. Map of study area, showing station locations for ICESCAPE cruises HLY1001 and HLY1101, as well as historical cruises listed in Table 1. The thick black contour represents the shelf break at 200 m depth, separating the shelf from the Canada Basin, and successively thinner contours represent the 1000 m, 2000 m, and 3000 m isobaths.

Table 1

Historical cruises used to determine seasonal evolution of depth of mixed layer and Chl *a* maximum on the Chukchi shelf and Canada Basin.

Cruise	Dates
HLY0201 HLY0203 NBP0304 HLY0303 HLY0402 HLY0403 HLY0404 HLY1003 HLY1103 HLY1203	May 6-July14 2002 July 17-August 26 2002 July 6-August 17, 2003 September 13-October 18, 2003 May 15-June 23 2004 July 19-August 25 2004 September 2-September 30, 2004 September 7-September 27, 2010 October 3-October 27, 2011 October 5-October 25, 2012

Samples for fluorometric analysis of Chl *a* were filtered onto 25 mm Whatman GF/F filters (nominal pore size 0.7 µm) placed in 5 mL of 90% acetone, and extracted in the dark at 3 °C for 24 h. Chl a was measured fluorometrically (Holm-Hansen et al., 1965) using a Turner Fluorometer 10-AU (Turner Designs, Inc.). Particulate organic carbon (POC) and nitrogen (PON) samples were collected by filtering subsamples onto pre-combusted (450 °C for 4 h) 25 mm Whatman GF/F filters. The filters were then immediately dried at 60 °C for 24 h and stored until processing. Prior to analysis for POC/PON, the samples were fumed in a dessicator with concentrated HCl, dried at 60 °C, and packed into tin capsules (Costech Analytical Technologies, Inc.) for elemental analysis on a Elementar Vario EL Cube or Micro Cube elemental analyzer (Elementar Analysensysteme GmbH, Hanau, Germany) interfaced to a PDZ Europa 20-20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, UK).

Net primary production (NPP) was assessed using simulated insitu (SIS) on-deck incubations. SIS NPP was determined by measuring ¹⁴C-carbon incorporation in water samples collected from multiple depths that were incubated at light intensities similar to those of the collection depth in the water column, in an on-deck incubator over a 24 h period. To 150 mL of sample, 0.74 MBq H¹⁴ CO₃⁻ was added and covered with 0–9 layers of neutral density screens to simulate light intensities of 85, 65, 25, 10, 5 and 1% of surface irradiance. After incubation, 30 mL was filtered in triplicate under very low vacuum (< 2.5 Hg). Filters were acidified with 0.1 mL 6 N HCl to drive off inorganic C. After 24 h, 5 mL of scintillation cocktail (Ecolume) was added and counted after > 3 h on a PerkinElmer Tri-Carb liquid scintillation counter. Total activity was determined on each sample by combining 50 μ L of sample with 50 μ L of ethanolamine, 0.5 mL filtered seawater and 5 mL of scintillation cocktail. Time zero samples were filtered (30 mL in triplicate) and acidified at the start of the incubation period.

2.3. Historical data

To acquire a robust seasonal dataset of SCM distributions in the Chukchi Sea and Canada Basin, we used CTD data from 10 additional cruises in this region over the past decade (Fig. 1). Table 1 lists the cruises, most of which were part of the multi-year interdisciplinary Shelf-Basin Interactions program (SBI); data are available at http://www.eol.ucar.edu/projects/sbi/. We utilized CTD-mounted fluorometer data (CTD fluorescence) to assess historical depth distributions of Chl a maxima. These historical fluorescence data were not calibrated to units of Chl a, but this is not a problem because we were interested only in the depth of the maximum, which is unaffected by calibration. Unfortunately, for historical cruises, we were unable to compare the depth of fluorescence maxima with the depth of discrete Chl a maxima. This is because it is unclear whether historical cruises targeted the SCM for discrete Chl a sampling (such that we would not necessarily expect the depth of fluorescence and discrete Chl a maxima to agree). However, as will be shown below, the depth of fluorescence and discrete Chl a maxima agreed closely during ICESCAPE, as well as in previous studies (e.g. Martin et al., 2010); therefore, we consider the depth of the CTD fluorescence maximum to be an effective proxy for the depth of the SCM (see Section 3).

We limited historical on-shelf data to west of 155 °W (off-shelf data west of 155 °W were retained), thereby excluding the Beaufort Shelf. Historical data were employed only in the analysis of the seasonal progression of the mixed layer depth (MLD) and SCM on the Chukchi shelf and Canada Basin; all other analyses are based solely on ICESCAPE data.

2.4. Sea ice retreat

Sea ice concentrations in the study region were determined from daily AMSR-E (Advanced Microwave Scanning Radiometer – Earth Observing System) data at 12.5 km resolution obtained from the National Snow and Ice Data Center (NSIDC). After projecting daily images onto an equal area grid of the Chukchi Sea using NASA's SeaWiFS Data Analysis System (SeaDAS), we determined the timing of sea ice retreat at each hydrographic station as the date when sea ice concentration first fell below 50%. We then calculated the time since ice retreat at each station as the difference in days between the date of shipboard sampling and the date of sea ice retreat.

2.5. Definitions and calculations

From 1 m binned CTD data, we calculated potential temperature (θ , °C) and potential density (σ_{θ} , kg m⁻³) referenced to the sea surface using the oceanography toolbox (*oce* package version 4.0) of the statistical computing program R. We then defined the mixed layer depth (MLD) as the shallowest depth at which σ_{θ} exceeded the surface value by 0.05 kg m⁻³ (Palmer et al., 2013) (Fig. 2).

We defined the percentage of surface PAR (%PAR) reaching each depth of the water column using the CTD-mounted PAR sensor as



Fig. 2. An example of water column profile from ICESCAPE cruise HLY1101, station 50 on the Chukchi shelf, showing the location, based on our definitions, of the Chl *a* maximum (green dashed line), the MLD (red dashed line), and the nitracline (black dashed line). Note that the CTD fluorescence axis is not shown. This station has a true SCM by our definition, as the Chl *a* maximum resides below the MLD. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

in Palmer et al. (2013). Euphotic depth was then defined as the depth where PAR was reduced to $\leq 1\%$ of surface PAR (Moran et al., 2005; Hill et al., 2005; Lee et al., 2007).

We defined the continental shelf as having a water depth of \leq 200 m; stations deeper than this were considered off-shelf (Brown et al., 2015). Surface waters were defined as the shallowest water sample taken at each hydrographic station, which was always within 5 m of the ocean surface. Similarly, we defined bottom waters as the deepest water sample taken at each hydrographic station on the Chukchi shelf, typically within 3 m of the ocean floor, determined by the rosette-mounted altimeter.

At each station, we defined the nitracline as falling halfway between the deepest bottle with $< 1 \mu mol L^{-1} NO_3^{-1}$ and the shallowest bottle with $> 1 \mu mol L^{-1} NO_3^{-1}$ (Fig. 2). We chose this $1 \,\mu$ mol L⁻¹ cutoff as it is the half-saturation constant for NO₃⁻ uptake employed in the models of Walsh et al. (2005) and Martin et al. (2013), and therefore accounts for the growth needs of Arctic phytoplankton. Note that because of the discrete nature of NO₃⁻ measurements, this definition lacks the higher vertical spatial resolution (1 m) of MLD and CTD fluorescence. Although this adds uncertainty to our calculated nitracline depth, we do not consider this to be an impediment to our interpretations, as we found that the nitracline depth was generally closely related to the SCM depth (see Section 3.3) as shown in previous studies using higherresolution nitrate sensors (e.g. Martin et al., 2010). We consider our on-shelf nitracline depths to be accurate within approximately \pm 5 m, and our off-shelf nitracline depths (where the nitracline was deeper and hence sampling resolution was reduced) to be accurate within approximately \pm 10 m.

2.6. Defining Chl a maxima and SCM

For each station, we defined the Chl *a* maximum as the depth where the CTD-mounted fluorometer trace reached its water column maximum, the same definition employed in previous detailed field studies of the SCM (Martin et al., 2010, 2012, Joo et al., 2012) (Fig. 2). This definition has the key advantages of consistency with these recent studies, high vertical resolution, simplicity, and ease of comparison to historical cruises (regardless of calibrations to Chl *a*). However, this definition also has at least two potential disadvantages. The first is fluorescence quenching, the reduction of the fluorescence signal in surface waters during the daylight hours around noon (e.g. Falkowski and Kolber, 1995), which may lead to spurious subsurface fluorescence maxima in daytime profiles. We found no relationship between surface fluorescence and time of day (p=0.34), indicating that daytime surface quenching was not a significant problem; Martin et al. (2010) also found surface quenching to be negligible in the Canadian Arctic. The second potential disadvantage of this definition is that it will assign Chl a maxima even at stations with homogeneous Chl a profiles, simply due to noise in the fluorescence signal. By analyzing profiles of discrete Chl a, we found that truly homogeneous Chl *a* profiles were exceptionally rare: 98.7% of ICESCAPE stations had a Chl *a* profile range of at least 0.1 μ g L⁻¹ (well within the detection limits of our shipboard fluorometer, \sim 0.025 µg L⁻¹), and therefore contained true Chl *a* maxima. Overall, this fluorometry-based definition of the Chl a maximum is the most appropriate due to the significant advantages listed above.

Further, it is important to define what makes a Chl *a* maximum a SCM, as it has remained unclear in previous studies exactly how deep a Chl *a* maximum must be in order to be considered part of the "subsurface." The SCM definition we have adopted here is as follows: a SCM is a Chl *a* maximum that is located below the MLD (Chl *a* maxima lying above the MLD were considered part of the

surface layer, not the subsurface). By this definition, the vast majority of ICESCAPE Chl *a* maxima were true SCM (see Section 3).

2.7. Calculating euphotic depth using a spectral light propagation model

Downward spectral light propagation through the water column was calculated using the Beer–Lambert Law and the inherent optical properties (absorption and backscatter) of Arctic waters. For each wavelength from 400 to 700 nm, we calculated the diffuse attenuation coefficient K (m⁻¹) as

$$K(\lambda) = (a_{ph} * (\lambda)(\text{Chl } a) + b_p(\lambda) + a_{CDOM}(\lambda) + a_d(\lambda) + a_w(\lambda) + b_w(\lambda))/\mu$$
(1)

where a_{ph}^* (m² mg Chl a^{-1}) is the Chl *a*-specific absorption coefficient for microalgae, b_p (m⁻¹) is the backscatter by microalgae (Whitmire et al., 2010), a_{CDOM} (m⁻¹) is the absorption by chromophoric dissolved organic matter (CDOM; Matsuoka et al., 2015), a_d (m⁻¹) is the absorption by detritus, and b_w and a_w (m⁻¹) are the backscatter and absorption of pure water (Smith and Baker, 1981), respectively, and μ is the mean cosine for downwelling irradiance (taken as 0.65 in this study). The quantity a_{ph}^* was calculated from ICESCAPE optical data (B.G. Mitchell, unpublished data) as $(a_p - a_d)$ /Chl *a*, in which a_p (m⁻¹) is total particulate absorption. All of these parameters were assumed to be constant throughout the surface water column above the Chl *a* maximum. From this model, euphotic depth (z_{eu} , m), or the 1% light depth, was calculated as $z_{eu} = \ln(0.01)/K$.

We ran the model using Chl *a* concentrations in Eq. (1) ranging from 0 to 3 μ g L⁻¹, (covering the range observed in ice-free surface waters during ICESCAPE cruises), and using three sets of spectral CDOM absorption coefficients as observed on ICESCAPE (Matsuoka et al., 2015): 1. Chukchi shelf mean, 2. Canada Basin mean, and 3. no CDOM.

All data analyses, plotting, and modeling were carried out in the statistical computing program R, version 2.13.0 (R Development Core Team, 2011).

3. Results

3.1. Mixed layer depth, nitracline, and euphotic depth

On the ICESCAPE cruises (June–July of 2010 and 2011), the MLD was highly variable across the Chukchi Sea shelf, ranging from 4 to 39 m, with a mean value of 11.2 ± 6.7 m in 2010 and 12.0 ± 6.5 m in 2011 (Fig. 3A and B). In rare cases (2% of stations), the MLD reached the bottom of the shallow shelf water column, such as in Bering Strait in 2010. There was no discernable latitudinal pattern in MLD; however, the MLD was slightly deeper on the Chukchi Shelf than off-shelf in the Canada Basin, both during the ICESCAPE cruises (two-sided Student's *t*-test, *p* < 0.001), and for all historical data (*p*=0.021). Our historical data show that the MLD on the Chukchi shelf averages 24 m in May, shallows to an average of 10 m by July (similar to the timing and results of the ICESCAPE cruises), then slowly deepens again to an average of 19 m in October (data not shown).

The depth of the nitracline was weakly but significantly correlated with MLD across the Chukchi shelf (r=0.178; p=0.011), and was generally far deeper and more variable than the MLD (Fig. 4B). The mean nitracline depth was 25.7 ± 12.6 m in 2010 and 23.9 ± 10.3 m in 2011 (Fig. 3C and D). Accordingly, NO₃⁻ was generally depleted within the mixed layer, averaging 0.2 ± 1.0 µmol L⁻¹, while concentrations below the MLD averaged 5.9 ± 5.8 µmol L⁻¹. The nitracline was far deeper off-shelf in the Canada Basin than on-shelf, averaging 44.7 ± 15.4 m (Fig. 3D). This

reflects the fact that off-shelf, NO₃⁻ concentrations remain perennially low within the thick, buoyant, low-salinity polar mixed layer due to low wintertime replenishment (Codispoti et al., 2005).

Euphotic depth on the Chukchi shelf was shallower in the west (\leq 25 m) than in the east (\geq 30 m) (Fig. 3E and F), likely due to the influence of nutrient-rich Anadyr water flowing through the western side of Bering Strait, promoting intense phytoplankton growth and curtailing light penetration into the deeper water column (e.g. Sambrotto et al., 1984). This is reflected in the strong positive correlation between euphotic depth and nitracline depth (Fig. 4C; p < 0.001), especially off-shelf where both plunge to > 40 m (Fig. 3D and F) as persistent NO₃⁻ depletion in the upper water column of the Alaska Coastal Current and Canada Basin prevents large phytoplankton blooms, allowing deeper light penetration. During ICESCAPE, the euphotic depth was half as deep on the Chukchi shelf (28.4 ± 10.0 m) as it was off-shelf (56.6 ± 14.4 m).

3.2. CTD fluorescence as a proxy for Chl a and phytoplankton biomass maxima

During the ICESCAPE cruises, we collected numerous metrics of phytoplankton biomass, including POC, PON, and Chl *a* at discrete depths, as well as CTD rosette-mounted transmissometer and fluorometer traces. Due to its high vertical resolution compared to discrete samples, as well as its usefulness in comparing to historical cruises for which discrete samples may not be available, CTD fluorescence is the optimal tool for determining the depth of the Chl *a* maximum. However, in utilizing this tool, it is important to determine how closely its depth discrete Chl *a* reflects true phytoplankton biomass as opposed to photoacclimation.

The depths of CTD fluorescence and discrete Chl a maxima on ICESCAPE were significantly correlated (p < 0.001; $R^2 = 0.53$), generally lying along the 1:1 line, with a slope of 0.94 (Fig. 5A). Although there was some scatter, 70% of all stations agreed to within 5 m, and 81% of all stations agreed within 10 m. The strength of this relationship reflects the success of our targeted SCM sampling approach during ICESCAPE. We used real-time downcast fluorescence traces to sample water at the depth of the fluorescence maximum, which coincided with the depth of the Chl *a* maximum, as shown by discrete samples. It is unlikely that sampling only at standard depths without this targeted approach would find such a strong correlation between the depth of the fluorescence maximum and the depth of the discrete Chl a maximum, because discrete sampling at standard depths would often miss the SCM altogether. Nevertheless, this relationship shows that the depth of the CTD fluorescence maximum indeed reflects the true depth of the Chl a maximum (Fig. 5A).

Given the capacity of phytoplankton to alter their cellular concentration and rate of synthesis of Chl a in response to changing environmental conditions, it is also important to determine how well the Chl *a* maximum reflects the phytoplankton biomass maximum. Martin et al. (2010) found that transmissometry was an effective proxy for phytoplankton biomass in Baffin Bay, but they note that it performs poorly in shallow, river-influenced shelf environments. Therefore, we instead guantified phytoplankton biomass in terms of POC, due to its utility in relating to C-based primary production, as well as the importance of POC to the food web. The depth of discrete Chl a maxima was significantly correlated with the depth of POC maxima, with a slope of 0.89 (p < 0.001; $R^2 = 0.33$; Fig. 5B). Of all stations, 55% lay on the 1:1 line (i.e. maximum POC and Chl *a* were sampled from the same bottle), and 66% were within 10 m; however, there was significant scatter, likely reflecting the presence of high concentrations of detritus and terrigenous organic matter, as well as photoacclimation (i.e. a reduction in cellular C:Chl *a* ratio). We found that the C:Chl *a* ratio was significantly reduced in the SCM (120 ± 114 ; median=83) compared to surface waters (446 ± 484 ; median=338), which may



Fig. 3. Maps showing mixed layer depth, nitracline depth, and euphotic depth at each station on ICESCAPE cruises HLY1001 and HLY1101. Certain stations are missing in the nitracline panels where the nitracline could not be defined, because NO_3^- was either homogeneously high or homogeneously low throughout the water column. As in all following maps, the gray contour represents the shelf break at 200 m depth. As in maps to follow, the 2011 panels are larger because our sampling extended further east in that year.

help explain stations with shallower POC maxima than Chl *a* maxima (below the 1:1 line on Fig. 5B). Stations with deeper POC maxima than Chl *a* maxima (above the 1:1 line on Fig. 5B) may be partially

explained by high concentrations of detritus in deeper waters. These results show that the Chl a maximum often, but not always, reflects the phytoplankton biomass maximum (in terms of POC) on the



Fig. 4. A matrix of scatterplots from the ICESCAPE cruises, making pairwise comparisons between euphotic depth, mixed layer depth, depth of Chl *a* maximum, and nitracline depth. The 1:1 lines are shown. In all panels, the 60 m axis limit allows visualization of nearly all shelf data, but cuts off a number of the off-shelf points (black triangles), where these parameters (excluding MLD) were often deeper than 60 m.

Chukchi shelf. Significant scatter is to be expected given this shallow, river-influenced shelf environment and the dynamic relationship between phytoplankton carbon and Chl *a*.

Overall, these results allowed us to utilize historical records of CTD fluorescence as proxies for the true vertical distributions of Chl a and, in the majority of stations, phytoplankton biomass. Therefore, hereafter when discussing the depth distribution of Chl a maxima, we will use CTD fluorescence unless otherwise noted. All reported Chl a concentrations are from discrete bottle samples.

3.3. Depth of the Chl a maximum

The depth of the Chl *a* maximum exhibited high variability across the Chukchi shelf (Fig. 6A and B), ranging from 3 to 106 m, with an average depth of 29.8 ± 15.5 m (30.3 ± 14.7 m in 2010 and 29.3 ± 16.1 in 2011). The vast majority of stations (241 of 269 shelf stations, or 90%) had true subsurface Chl *a* maxima (SCM) based on our definition (i.e. Chl *a* maximum deeper than MLD),

averaging 18.1 ± 16.5 m deeper than the MLD (Figs. 4D and 7). The depth of the Chl *a* maximum was not significantly linearly correlated with MLD (p=0.328; Fig. 4D), but was strongly correlated to nitracline depth (R=0.58; p < 0.001; Fig. 4F) and especially to euphotic depth (slope=0.86; p < 0.001; Fig. 4E). In fact, in both the shelf and Canada Basin environments, mean SCM depth was within 1 m of mean euphotic depth. Like the nitracline and euphotic depths, SCM depth was far deeper off-shelf in the Canada Basin, averaging 55.7 ± 18.8 m.

Using multiple linear regression (MLR) analysis we found that nitracline depth and euphotic depth individually explained 42% and 45% of the variance in SCM depth, respectively, and together explained 51% of the variance, while MLD added no explanatory power to the model, accounting for 0% of the variance in SCM depth.

Not only did the depth of the Chl *a* maximum vary greatly by station, but so did the Chl *a* concentration associated with the depth of the Chl *a* maximum, ranging from 0.2 to 77.0 μ g L⁻¹ on



Fig. 5. Scatterplots of (a) the depth of the Chl a maximum as recorded by discrete bottle samples vs. the CTD-mounted fluorometer, and (b) the depth of the POC maximum and the depth of the Chl a maximum from discrete samples. The black line represents 1:1, while the gray dashed line shows the least-squares regression line.

the Chukchi shelf (mean $10.7 \pm 13.2 \ \mu g \ L^{-1}$) (Fig. 6C and D). We observed a significant negative relationship between the depth of the Chl *a* maximum and its Chl *a* concentration, with deeper SCM having lower Chl *a* concentrations (*p* < 0.001) (Fig. 8).

In only 7% of stations was the Chl *a* maximum at the surface, while in 31% of stations (41 of 124 in 2010 and 43 of 145 in 2011) the SCM had penetrated all the way to the bottom waters of the shallow shelf. On the Chukchi shelf, surface Chl *a* averaged $2.7 \pm 6.8 \ \mu g \ L^{-1}$ (median 0.38), but when considering only ice-free stations (thus ignoring the massive under-ice bloom of 2011, which contained by far the highest surface Chl *a* concentrations), it averaged less than half this amount, $1.2 \pm 2.8 \ \mu g \ L^{-1}$ (median 0.35 $\ \mu g \ L^{-1}$) (Fig. 9A and B). Off-shelf, mean surface Chl *a* was far lower at 0.1 ± 0.2 (median 0.05 $\ \mu g \ L^{-1}$). We often observed substantial accumulations of Chl *a* in bottom waters, which

reached $>5 \ \mu g \ L^{-1}$ in 27% of shelf stations, especially in the shallow Hanna Shoal region in 2011 (Fig. 9C and D).

3.3.1. Seasonality of SCM depth

By combining ICESCAPE data with historical data collected from May to October, we observed the seasonal progression of the depth of the Chl a maximum on the Chukchi shelf and Canada Basin (Fig. 10; Table 2). In May, Chl a maxima were often near the surface on the Chukchi Shelf (15% in the upper 5 m and 50% in the upper 20 m; Fig. 10A), yet even this early in the year, SCM depth could reach > 40 m, such that the average was \sim 20 m, similar to off-shelf stations (Table 2). In June, Chl a maxima were distributed deeper than in May, with more spread in the data, both on- and off-shelf. By July and August, the distributions of shelf versus offshelf Chl *a* maxima had diverged, with the average depth of shelf Chl a maxima plateauing at 27–30 m (generally well above the shelf bottom), and off-shelf Chl *a* maxima extending deeper to \sim 40 m. These averages remained similar in September (Table 2), although in both shelf and off-shelf stations, more Chl a maxima were found nearer the surface as well as at great depth. By October, as summer stratification began to break down, Chl a maxima were distributed much shallower, including many surface Chl a maxima (Fig. 10F), likely due to re-introduction of nutrients to surface waters.

3.3.2. SCM relationship to net primary production

The depth of the NPP maximum (as determined by on-deck SIS experiments during ICESCAPE) was significantly positively correlated to the depth of the Chl *a* maximum on the Chukchi shelf (r^2 =0.25; p=0.003), though it was only half as deep, averaging 15.0 ± 12.1 m (compared to 29.8 m for the SCM) (Fig. 11A–C). For our few off-shelf NPP stations (n=3), we found that the NPP maximum was more than twice as deep as in shelf waters (averaging 38.1 ± 20.4 m), but was still far shallower than the SCM (which averaged 55.7 m off-shelf).

At the time of these cruises (June–July), the SCM had greater rates of NPP than surface waters in 79% of stations; yet mean NPP at the SCM was not significantly higher than at the surface (NPP at the SCM averaged $90.9 \pm 116.0 \text{ mg C m}^{-3} \text{ d}^{-1}$ while NPP at the surface averaged $62.4 \pm 124.1 \text{ mg C m}^{-3} \text{ d}^{-1}$; paired student *t*test, p=0.31; Fig. 11D). This lack of statistical difference between mean surface and SCM NPP was due to a few surface samples with high rates of NPP (> 100 mg C m⁻³ d⁻¹; Fig. 11D), and it persisted even when the high surface productivity stations of the massive under-ice bloom of 2011 were removed (p=0.22).

3.3.3. Relationship of SCM depth to sea ice retreat

The timing of sea ice retreat is likely to be an important signal that guides the seasonal development of the SCM. As sea ice thins, develops surface melt ponds, and finally retreats, it allows successively more light to penetrate; thus, the timing of sea ice retreat is related to the amount of light reaching the upper water column (whether through the ice or open water), and can provide a proxy that is readily observable by satellite for the onset of NPP.

When considering all stations across the Chukchi shelf, we observed no relationship between the time elapsed since sea ice retreat and the depth of the Chl *a* maximum (Fig. 12 gray dots). However, when considering only "pronounced" Chl *a* maxima (i.e. stations with a Chl *a* maximum at least $5 \ \mu g \ L^{-1}$ greater than the station minimum; Fig. 12 black diamonds), the Chl *a* maximum deepened significantly with time since sea ice retreat (p < 0.001). Although there was a large amount of scatter, the least-squares regression line shows that the SCM reached ~30 m approximately 1 month after sea ice retreat, descending at a rate of ~0.4 m d⁻¹ (Fig. 12). Interestingly, the *x*-intercept of this relationship (i.e. the



Fig. 6. The depth (m; panels a and b) and concentration (µg Chl *a* L⁻¹; panels c and d) of the Chl *a* maximum on the Chukchi shelf and Canada Basin during 2010 and 2011 ICESCAPE cruises.



Fig. 7. Comparison of the depth of the MLD and Chl *a* maxima on the Chukchi shelf during the 2010 and 2011 ICESCAPE cruises. Blue colors (negative values) show Chl *a* maxima below the MLD (i.e. true SCM), while reds (positive values) show Chl *a* maxima above the MLD.



Fig. 8. Scatterplot of the depth of the Chl *a* maximum on the Chukchi shelf vs. the Chl *a* concentration at that maximum. Diamonds show the means of Chl *a* concentration binned every 10 m depth, with standard deviations plotted.

point at which the Chl *a* maximum was at the ocean surface) was approximately -30 days, suggesting that the surface phytoplankton bloom begins a full month prior to sea ice retreat (see Palmer et al., 2014 for a modeling analysis of the seasonal cycle of primary productivity in this region). By the time of sea ice retreat, the depth of the Chl *a* maximum had already reached ~ 15 m.

3.4. Euphotic depth analysis

Based on our spectral model of the penetration of PAR into the water column of the Chukchi shelf, the euphotic depth shallows with increasing surface Chl *a* (Fig. 13). However, this shoaling of euphotic depth is gradual, and slows asymptotically at higher surface Chl *a* concentrations, especially above $1 \ \mu g \ L^{-1}$. Because of this, even with a quadrupling of surface Chl *a* from 0.5 to $2 \ \mu g \ L^{-1}$, the range in modeled euphotic depth is relatively narrow (~25–35 m). Even when surface Chl *a* drops to 0, euphotic depth does not exceed 40 m. Our model agreed well with ICESCAPE field data from the Chukchi shelf: the mean surface Chl *a* (1.2 $\ \mu g \ L^{-1}$) and euphotic depth (28.4 m) we observed on the Chukchi shelf fell directly on the modeled line (Fig. 13).

The shallow euphotic depth and relative insensitivity to surface concentrations of Chl *a* on the Chukchi shelf is likely due to high concentrations of surface CDOM. When modeling light penetration using the lower surface CDOM concentrations of the Canada Basin, euphotic depth reached > 50 m and its shoaling with increasing Chl *a* was steeper. Again, the model closely matched our observations in the field, with the average euphotic depth in the Canada Basin (56.6 m) being only a few meters shallower than the modeled result at the same mean surface Chl *a* (0.1 µg L⁻¹) (Fig. 13). When CDOM was removed from the model, light penetrated deeper still, with euphotic depth reaching 100 m when the Chl *a* concentration was set to zero (not shown).

We used our model to assess the relative importance of CDOM and Chl *a* in attenuating light on the Chukchi shelf by holding shelf CDOM constant and increasing Chl *a* step-wise. CDOM remained the most important factor limiting light penetration until Chl *a* climbed to $\geq 1.4 \,\mu g \, L^{-1}$, at which point Chl *a* became more important. When repeating this analysis for the Canada Basin,

where CDOM concentrations are far lower, Chl *a* became the most important factor limiting light penetration at Chl *a* concentrations of only 0.2 μ g L⁻¹.

4. Discussion

4.1. Optimality of SCM depth

In the Arctic Ocean, the emerging paradigm for the development in summer of the ubiquitous SCM can be summarized as follows: when the water column stratifies in spring, a surface bloom begins and depletes available NO_3^{-} in the upper water column. The Chl a maximum gradually migrates deeper, depressing the nitracline until it approaches the compensation depth (the point at which primary productivity and respiration are balanced), where, acclimated to the low light conditions of the subsurface, it continues to grow actively with a relatively high f-ratio (Martin et al., 2010, 2012; Ardyna et al., 2013; Palmer et al., 2013). In this paradigm, the SCM represents the optimal depth for phytoplankton growth with respect to two opposing gradients: that of light from above and that of NO₃⁻ from below. This conceptual model has largely been developed through field and modeling studies in the Beaufort Sea and Canadian Arctic Archipelago; a major goal of the present study was to determine whether field data from the Chukchi Sea are consistent with a dynamic and actively growing SCM maintaining its optimal position in the water column.

Overall, our data support the above paradigm. Several lines of evidence rule out a passively sinking, aged post-bloom community. First, as shown by Palmer et al. (2013), the SCM community of the Chukchi shelf is physiologically acclimated to the low light environment of the subsurface, with increased Chl *a* content and photosynthetic efficiency. Second, as will be discussed below, the SCM was active in terms of NPP during our June–July ICESCAPE cruises. Third, as will also be discussed below, the SCM does not continue progressing downward throughout the season, but remains at \sim 30 m throughout the peak summer months, inconsistent with phytoplankton sinking. Most importantly, the depth of the SCM was highly correlated with both nitracline depth and euphotic depth, which would not be expected from a passively sinking community of cells, but would be expected from a community that actively maintains its optimal position with respect to its needs for growth.

It is surprising that in our analysis, SCM depth was completely independent of the MLD. MLD and SCM shared no linear correlation (Fig. 4D), and multiple linear regression showed that MLD explained 0% of the variance in SCM depth, compared to 51% for both nitracline depth and euphotic depth. Previous studies suggested that the pycnocline is co-located with the nitracline (i.e. the pycnocline separates the nutrient-poor surface mixed layer from the nutrient-rich subsurface layer), and therefore the SCM forms at the base of the pycnocline (Harrison et al., 1982; Carmack et al., 2004; Hill et al., 2005) or within the pycnocline itself (Stabeno et al., 2012). However, in our study, the nitracline and SCM were both located far deeper than the MLD (Figs. 4 and 7), apparently below the influence of surface mixing, similar to Martin et al. (2010). Stratification is likely important in initiating surface blooms in the spring on the Chukchi shelf, but as spring moves into summer, the MLD shallows while the SCM deepens, and by June the SCM is already twice as deep as the MLD (26.5 m compared to 13.0 m), remaining substantially below the MLD throughout the growth season. Because the role of water column physics in setting SCM depth appears small, this underscores the dual role of light and nutrients in setting the optimal depth for SCM development.

An important question for understanding the dynamics of the SCM, and one that has not been specifically addressed to our knowledge, is how this feature maintains its position in the water column (especially given that it is far below the pycnocline). One



Fig. 9. Surface (panels a and b) and bottom water (panels c and d) Chl *a* concentrations on the Chukchi shelf on ICESCAPE cruises in 2010 and 2011. Note the different scales on these plots: the surface Chl *a* scale ranges from 0 to $\geq 1 \ \mu$ g Chl *a* L⁻¹; bottom Chl *a* from 0 to $\geq 5 \ \mu$ g Chl *a* L⁻¹.

possibility is active buoyancy regulation by diatom cells, providing the ability to migrate with the nitracline. For example, Booth et al. (2002) showed that Chaetoceros socialis in the North Water Polynya maintained its population within the euphotic layer for up to three months through adaptations for buoyancy regulation. Because the cells are small, spiny, and lightly silicified, they do not readily sink out of the upper layer. However, when conditions deteriorate, they can sink by forming aggregates or heavily silicified resting spores until encountering favorable growth conditions, at which point they can quickly cease sinking and resume active growth. Another possible mechanism by which the SCM could maintain its position is through a dynamic balance between the rates of phytoplankton growth and losses (e.g. sinking, grazing, viral lysis), as suggested by Tremblay et al. (2008). Put simply, at the SCM, growth rates are highest and exceed losses, allowing for biomass accumulation, while in other parts of the water column losses exceed growth rates, precluding biomass accumulation. In this scenario, there may be constant sinking loss of cells from the SCM, even as the SCM as a whole maintains its position through active growth where light and nutrients are optimal.

Our data suggest that on the Chukchi shelf, the former mechanism of buoyancy regulation is of secondary importance. If all cells are capable of regulating their buoyancy and remaining at the optimal depth, we would expect that as they migrate deeper, depressing the nitracline through continual new production, this optimal layer should continue to accumulate more and more phytoplankton biomass throughout the season. This is opposite of what we observed: phytoplankton biomass is actually reduced in deeper SCM (Fig. 8). This lack of phytoplankton biomass accumulation indicates that it is the latter mechanism of phytoplankton growth rates equaling or exceeding losses that allows the SCM to maintain its optimal position within the water column. If so, this suggests that (1) deeper SCM have lower biomass compared to shallower SCM because growth rates are reduced in the lower light environment (assuming constant losses), and (2) the significant new production associated with the deepening of the nitracline does not accumulate in the SCM, and therefore may constantly be sinking to the seafloor as export production.

4.2. Seasonal progression of SCM and relationship to under-ice blooms

This is the first study to combine new and historical data to document the seasonal progression of SCM in the Chukchi Sea. Although there was strong variability in SCM depth every month having available observations (May–October; Fig. 10), the general



Fig. 10. Seasonal comparison of depth distributions of Chl *a* maxima on the Chukchi shelf and Canada Basin, utilizing all historical data as described in Methods. For each monthly panel, the bin from 80 to 85 m depth also includes all SCM > 85 m depth.

Table 2

Monthly progression of depth of CTD fluorescence maxima in of the Chukchi Sea shelf and Canada Basin.

	Chukchi Shelf			Canada Basin		
	Mean	Median	Standard deviation	Mean	Median	Standard deviation
May	23.5	20.5	13.4	20.0	20.0	7.2
June	26.5	25.0	15.5	29.8	27.5	21.9
July	29.7	27.0	15.8	40.9	37.0	17.0
August	26.9	25.0	10.1	38.6	36.0	13.4
September	27.7	28.0	14.1	36.4	38.0	17.6
October	22.3	21.5	10.9	24.3	20.0	15.9

pattern on the Chukchi shelf was a relatively shallow distribution in May, followed by deepening, maintenance of SCM depth at \sim 30 m in peak summer, and shallowing again in October. This pattern is consistent with a conceptual model of blooms driven initially by abundant surface nutrients, followed by SCM development associated with a deepening nitracline, followed by fall storms that erode summer stratification and reintroduce shallow new nitrogen, promoting blooms near the ocean surface (Martin et al., 2012, 2013).

The gradual development of SCM on the Chukchi shelf over 2–3 months contrasts with the rapid development in the Beaufort Sea and CAA (Tremblay et al., 2008). For example, Palmer et al. (2011) observed SCM deepening from 10 to 34 m within six days in the Beaufort Sea, a process that takes closer to two months in the Chukchi Sea. This difference in SCM development is almost certainly due to the perennially low surface nutrients in the CAA, such that the best growth conditions are found at depth, even at the start of the season (Tremblay et al., 2008).

The rate of SCM descent after the initial surface bloom is important to understand when characterizing the seasonal development of the SCM. Between May and July, the SCM deepened from 0–20 m to ~30 m over 60 days, yielding a descent rate of ~0.2–0.5 m d⁻¹ based on the historical data only. This analysis is reinforced by our own data from ICESCAPE, showing a deepening rate based on the timing of sea ice retreat of 0.4 m d⁻¹ (Fig. 12). These rates are slower than the rate of SCM deepening in the Bering Sea of 1.0 m d⁻¹ (Iverson et al., 1979).

Interestingly, the relationship between SCM depth and the timing of ice retreat shows that the Chl *a* maximum is at the surface approximately one month before sea ice retreat (Fig. 12). This is the signature of under-ice blooms fueled by light penetration through surface melt ponds, which were recently documented in this region in the field (Arrigo et al., 2012), in a recent numerical modeling study (Palmer et al., 2014), and over a 15-year time series from 1998 to 2012 using satellite data (Lowry et al., 2014). As suggested by Palmer et al. (2013), many of the SCM we observed in open waters of the Chukchi shelf are likely remnant under-ice blooms, and may be preacclimated to the low light conditions of the subsurface (having developed in the low-light under-ice environment). Thus, SCM development in the current primary production regime of the Chukchi Sea is likely inextricably tied to under-ice blooms.

By the time sea ice finally retreats, the SCM has already reached \sim 15 m depth, too deep to be observed by satellite ocean color sensors (which observe approximately the first optical depth, or \sim 3 m based on the mean attenuation coefficient we observed in surface waters of the Chukchi shelf), thus leading to a drastic underestimate of NPP in satellite-based studies (Arrigo et al., 2014; see also Lowry et al., 2014). This is superficially similar to the Beaufort Sea and CAA, where the SCM may already be well developed at the time of sea ice retreat (e.g. Tremblay et al.,



Fig. 11. Panels a and b show a comparison of the depths of the NPP maximum and Chl *a* maximum, with blue colors showing NPP maximum shallower than the SCM. (Panel c) Scatterplot of the depth of the NPP vs. Chl *a* maximum, with the 1:1 line shown in black and the least-squares regression line shown in red. (Panel d) Boxplot of surface versus SCM volumetric rates of net primary productivity (mg C m⁻³ d⁻¹). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

2008). However, the mechanism of development is likely to be fundamentally different. In the Beaufort Sea and CAA, the early SCM develops in response to perennially low surface nutrients, while in the Chukchi, it is a consequence of under-ice blooms depleting surface nutrients prior to ice retreat (Palmer et al., 2014).

4.3. Limits to SCM depth

In oligotrophic regions of the global ocean, such as the subtropical North Pacific and tropical Western Pacific, the SCM may reach 150 m (Shulenberger and Reid, 1981; Furuya, 1990). In contrast, in our study on the Chukchi shelf, the median depth of the SCM never exceeded 30 m, reaching this depth by July and remaining there for three months, throughout the peak of the Arctic summer. This depth is remarkably similar to that reported in previous studies undertaken across the pan-Arctic shelves throughout the summer months (Table 3), suggesting that there is a consistent physical or chemical limit to SCM depth on Arctic shelves, constraining it to remain within \sim 30 m of the surface. It is crucial to understand what drives this very shallow limit to SCM depth across the Arctic shelves.

One possible explanation for this limit to SCM penetration is that in the short Arctic growing season, 30 m is simply as deep as the SCM has time to reach before the onset of fall storms and loss of stratification. However, this can easily be ruled out by our seasonal progression analysis, showing that the SCM reaches 30 m by early summer, with plenty of time remaining to deepen further and utilize the remaining NO_3^- below it. Likewise, nutrient availability is unlikely to be responsible for this depth limit, as we consistently observed high NO_3^- concentrations below the SCM, such that phytoplankton should be able to continue deepening and utilizing NO_3^- below 30 m if not limited by some other factor. Therefore, the cause of the regular 30 m limitation of the SCM on Arctic shelves is likely to be light availability.

During the ice-free, river-influenced summer months, surface waters of the Chukchi shelf have relatively high concentrations of both Chl *a* and CDOM. Together, these constituents make surface waters optically thick, severely curtailing light penetration. Our spectral model agreed closely with observations made during ICESCAPE, showing that at the mean surface Chl *a* concentration on the Chukchi shelf $(1.2 \ \mu g \ L^{-1})$, euphotic depth was limited to



Fig. 12. Scatterplot of the depth of the Chl *a* maximum vs. the time elapsed since sea ice retreat on the Chukchi shelf. Gray dots show all data, while black diamonds show pronounced SCM, defined as having Chl *a* concentrations at least $5 \,\mu g \, L^{-1}$ greater than the minimum measured at the same station. The least-squares regression line is shown.



Fig. 13. Results of a spectral model of light penetration through the water column, showing how euphotic depth (1% light level) varies with surface Chl *a* concentration. Results of three model runs are shown, employing mean CDOM absorption spectra for the Chukchi shelf (white), the Canada Basin (gray), and with CDOM completely removed (black). The white and gray crossed points show ICESCAPE observed mean surface Chl *a* and euphotic depth for the Chukchi shelf and Canada Basin, respectively.

~30 m (Fig. 13). Even when we reduced surface Chl *a* to 0, modeled euphotic depth was less than 40 m, demonstrating the crucial importance of CDOM in limiting light penetration on the Chukchi shelf. Our model showed that CDOM attenuated light as effectively as a Chl *a* concentration of ~1.4 µg L⁻¹ (similar to the mean surface Chl *a* observed). Hence, at typical surface Chl *a* concentrations, Chl *a* and CDOM contribute roughly equally to light attenuation on the Chukchi shelf (with Chl *a* playing an increasing role at higher concentrations). This is nearly identical to the results of Hancke et al. (2014) from the Barents Sea, where Chl *a* concentrations of ~1 µg L⁻¹. The agreement between our spectral

model and ICESCAPE observations extended into the Canada Basin, where lower CDOM concentrations and mean surface Chl *a* (0.1 µg L⁻¹) allowed greater light penetration, leading to a significantly deeper mean euphotic depth of > 55 m (Fig. 13), similar to the results of Lee and Whitledge (2005). Here, too, we observed that at typical surface Chl *a* concentrations, Chl *a* and CDOM had roughly equal impacts on light penetration into the water column.

In turn, euphotic depth appeared to be the primary driver of SCM depth during ICESCAPE (Fig. 4E), with the mean SCM and euphotic depths agreeing to within 1 m on both the Chukchi shelf and Canada Basin. This is consistent with previous Arctic studies noting the co-location of the SCM with the base of the euphotic zone (e.g. Harrison et al., 1982; Kristiansen and Lund, 1989; Martin et al., 2013).

Other Arctic shelves are likely to be optically similar to the Chukchi shelf during summer, with relatively high concentrations of Chl *a* and CDOM strongly limiting the penetration of light. For example, Harrison et al. (1982) observed mean surface Chl *a* concentrations of 0.6–1.0 μ g L⁻¹ in Baffin Bay in late summer (similar to our mean value of 1.2 μ g L⁻¹), and Hancke et al. (2014) observed high summer concentrations of CDOM throughout the Barents Sea. Moreover, our analysis demonstrates that due to high CDOM concentrations, euphotic depth on Arctic shelves is relatively insensitive to the amount of surface Chl *a*. Modeled euphotic depth occupied a narrow depth range (~25–35 m) across a wide range of surface Chl *a* values typical of Arctic shelves during summer (Fig. 13). This likely explains why previous studies across the pan-Arctic shelves have been so remarkably consistent in finding summer SCM depths of approximately 30 m (Table 3).

Because surface Chl *a* plays an important role (roughly equal to that of CDOM at typical concentrations) in limiting euphotic depth and, in turn, SCM depth across the pan-Arctic shelves, it is important to understand the origin of this surface Chl a. It is unclear how $> 1 \mu g$ Chl a L⁻¹ is maintained in nutrient-depleted surface waters. One possibility is that a small amount of phytoplankton biomass may be mixed up into surface waters from the upper SCM. This can be ruled out, as the SCM averaged ~ 18 m deeper than the MLD, putting it out of range of surface mixing (Fig. 7). Another possibility is that this surface Chl a may be dominated by slowly sinking small phytoplankton whose growth is fueled by regenerated NH4⁺ released by heterotrophs and remineralized organic matter. We observed $0.1 + 0.3 \mu mol L^{-1}$ NH₄⁺ in surface waters of the Chukchi shelf, and this level of accumulation indicates that significant nutrient recycling may be at work in surface waters. This is consistent with Hill and Cota (2005) and Hill et al. (2005) who observed a surface community of small-celled chlorophytes and prasinophytes at the surface during summer, indicative of regenerated production. Given the importance of surface Chl *a* to the dynamics of the SCM, understanding its origin will be an important theme for future research. Our analysis demonstrates that surface and subsurface Chl a are not independent, but that surface Chl a strongly influences the subsurface Chl *a* growth environment by altering the penetration of light.

The fact that high surface Chl *a* and CDOM concentrations curtail light penetration on the Chukchi Shelf (and almost certainly other Arctic shelves as well) may profoundly limit total new production, for it suggests that NO_3^- below 30 m depth is unlikely to be utilized over the growth season. Given an average depth of Arctic shelves of 50 m, if we assume that NO_3^- is evenly distributed throughout the water column in early spring, a SCM depth limit of 30 m would leave 40% of NO_3^- unutilized, reducing new production by the same percentage. Put another way, if concentrations of post-bloom surface Chl *a* and CDOM were lower on Arctic shelves, clearing the waters for deeper light penetration, new production could potentially be 40% greater.

Table 3

Depth of Chl a maxima in previous Arctic studies.

	Shelf	Off-Shelf		
	Location	SCM Depth (m)	Location	SCM Depth (m)
Harrison et al. (1982)	Baffin Bay	34		
Cota et al. (1996)	North Chukchi Slope	30-40		
Heiskanen and Keck (1996)	Laptev Sea	30		
Hill and Cota (2005) ^a	Chukchi Sea	31		
Carmack et al. (2004)	Beaufort Sea	25-30		
Iverson et al. (1979)	Bering Sea	30		
Stockwell et al. (2001)	Bering Sea	26 ^b		
Martin et al. (2010)	Canadian Arctic	29	Canada Basin	≤ 62
Martin et al. (2012)	Canadian Arctic	35		
Tremblay et al. (2008)	Beaufort Sea	30-57		
Ardyna et al. (2011)	Beaufort Sea; Canadian Arctic Archipelago; Baffin Bay	26; 24; 37		
Lee and Whitledge (2005)			Canada Basin	50-60
McLaughlin and Carmack (2010)			Canada Basin	\sim 47–65
Coupel et al. (2011)	Chukchi Sea	22	Canada Basin	60
This Study	Chukchi Sea	29.8	Canada Basin	55.7
Average		30.7 ± 5.5		56.7 ± 2.2

^a For consistency with this study, we report SCM depth from the CTD-mounted fluorometer, rather than bottle samples (which averaged 25 m).

^b Average obtained from Table 1.

4.4. Productivity of the SCM

The productivity of the Arctic SCM has been a matter of substantial debate. This debate has centered around the use of satellite-based NPP algorithms, which generally do not capture the SCM. Arrigo et al. (2011) and Ardyna et al. (2013) have shown that satellite-based annual depth-integrated Arctic NPP is quite insensitive to the presence of the SCM; on the other hand, Tremblay et al. (2008) reported that perhaps half of the seasonal NO₃ production was mediated by the SCM in the southeastern Beaufort Sea, and the recent modeling study of Martin et al. (2013) from the same region shows that the SCM is responsible for 65-90% of annual NPP. It is very important to recognize that these seemingly conflicting results can be reconciled: the SCM may be highly productive without causing substantial error in satellite-derived NPP. This is because, in contrast to what is commonly assumed, satellite algorithms do not ignore NPP in the subsurface layer; rather, they calculate NPP at all depths using a prescribed Chl a depth profile that does not include a SCM. The error associated with using this prescribed profile gets smaller at higher surface Chl *a* concentrations, which typify Arctic waters as described above. Therefore, although satellite algorithms do not explicitly include a SCM, they nevertheless capture most NPP occurring even in the subsurface layer (see Arrigo et al., 2011, Figs. 5 and 6). This distinction should be recognized in future discussions of the productivity of the Arctic SCM.

Our rate of SCM deepening (Section 4.2) allows us to estimate new production by the SCM during the early part of the growth season as the SCM depresses the nitracline. Assuming NO₃⁻ concentrations of 15 μ mol L⁻¹ (Mills et al., 2015), typical for the nutrient-rich central/western Chukchi Sea where most of the "pronounced" Chl a maxima were observed (Fig. 12), our SCM deepening rate (0.4 m d⁻¹) indicates a new production rate of $6 \text{ mmol N m}^{-2} \text{d}^{-1}$, or (assuming a C:N ratio of 6.6), \sim 475 mg C m⁻² d⁻¹ during SCM deepening in the spring. Employing the f-ratio observed by Martin et al. (2012) at the SCM in spring (0.74) this gives a NPP rate of \sim 640 mg C m⁻² d⁻¹. This is at least double the NPP rate that Hill and Cota (2005) found on the Chukchi shelf in spring ($<300\ mg\ C\ m^{-2}\ d^{-1}$), but productivity during their study was light-limited due to heavy ice cover, such that the SCM may not yet have been actively deepening the nitracline. It is likely that this period of SCM deepening between May and July is when most new production on the Chukchi shelf takes place (similar to Tremblay et al., 2008; Martin et al., 2013), and that after the SCM stops deepening in July, the rate of new production slows considerably.

SCM deepening was largely complete by the time we sampled the Chukchi shelf on ICESCAPE (it had reached 30 m, the approximate SCM depth limit shown by historical data and previous studies). At this time, volumetric NPP rates in the SCM averaged \sim 90 mg C m⁻³ d⁻¹. Using the *f*-ratio observed by Martin et al. (2012) at the SCM in summer (0.37) gives a SCM new production rate of \sim 33 mg C m⁻³ d⁻¹. This is similar to the modeled new production rate of Martin et al. (2013) after the SCM had reached 30 m, \sim 25 mg C m⁻³ d⁻¹ (calculated from their reported rate of 0.20 mmol N m⁻³ d⁻¹ using their C:N ratio of 10.3). This continuous new production after the SCM stops deepening in summer is likely driven by upward diffusion and mixing of NO₃⁻ enabled by the SCM's close association with the nitracline. Moreover, this new production at the SCM in summer is almost certainly necessary to maintain the SCM layer, equaling or outpacing the continuous losses to sinking, grazing, and viral lysis.

Unfortunately, because our ICESCAPE field data span a limited time of year, this precludes quantifying the SCM's contribution to Chukchi Sea annual integrated NPP, to assess whether it is of the same large magnitude observed in the Beaufort Sea and CAA (Martin et al., 2013). However, we consider it likely that the SCM contributes a lower fraction of annual integrated NPP in the Chukchi Sea compared to the Beaufort for two reasons. First, the Chukchi Sea has a high pre-bloom surface nutrient load, leading to intense and long-lived surface blooms, both in open water (Arrigo and van Dijken, 2011) and under the ice pack (Arrigo et al., 2012), suggesting a greater contribution of surface production in spring compared to the Beaufort Sea. Second, during summer, we observed that the productivity maximum in the Chukchi Sea was located significantly shallower than the SCM (by an average of 16 m; Fig. 11), likely due to sub-saturating irradiance levels at the SCM. This is consistent with Cota et al. (1996), who found the SCM in the northern Chukchi Sea in summer ranged from 31 to 58 m, while the photosynthetic maximum was far shallower, at 4-22 m.

We suggest the following conceptual model for the contribution of the SCM in the Chukchi Sea: surface blooms dominate productivity in spring until surface NO_3^- is exhausted, at which point the SCM develops and dominates productivity as it deepens the nitracline. Once the SCM has reached 30 m in July, it remains at this depth and continues a modest level of productivity, likely accounting for most of the new (NO_3^-) production, but being significantly deeper than the NPP maximum.

During ICESCAPE, we found surprisingly large accumulations of Chl a in Chukchi shelf bottom waters (with 31% of shelf stations having their Chl *a* maximum at the bottom of the water column; Fig. 9C and D). Bottom water Chl *a* accumulations may be large because (1) the shelf bottom is shallow enough to be within the euphotic zone, allowing active growth in bottom waters, (2) physical processes such as sediment resuspension or lateral advection bring Chl *a* into bottom waters, or (3) constantly sinking organic matter produced nearer to the surface accumulates in bottom waters throughout the season. We found that it was relatively rare for Chukchi shelf bottom waters to be within the euphotic zone (with only 5% of shelf stations having euphotic depth penetrating to within 5 m of the bottom), suggesting that bottom Chl a may generally not be actively growing, unlike SCM that maintain their vertical position within the water column through active growth. Nevertheless, we found large amounts of fresh (i.e. not degraded) Chl *a* in bottom waters, suggesting that the organic matter was produced earlier in the same season, rather than re-suspended from shelf sediments. For these reasons, we suggest that these large Chl a accumulations in bottom waters are indicative of export production that accumulates in bottom waters throughout the season. There may be particularly large export in regions where the bottom depth shallows to near 30 m, such as Hanna Shoal (Fig. 9C and D). If, as we have suggested, the SCM is maintained by constant growth balancing or outpacing constant loss, export production at a low level may be continuous, allowing Chl a to accumulate in bottom waters below the SCM. Furthermore, as the growing season wanes and euphotic depths become shallower than their peak summer 30 m limit, the entire SCM community may cease to grow and be exported to the ocean floor, feeding a rich benthos and possibly leading to tight pelagicbenthic coupling. Understanding the relationship between the SCM and export production will be an important challenge to understanding the fate of fixed C on the Chukchi shelf.

5. Summary

In this first in-depth study of the SCM on the Chukchi Sea shelf and Canada Basin, our data are consistent with the emerging paradigm of an actively growing community that progressively deepens the nitracline until approaching the compensation depth for phytoplankton growth (e.g. Martin et al., 2010). The ubiquitous SCM should not be regarded as a sinking, post-bloom phenomenon, but an active and dynamic community that optimizes its position with respect to its growth needs of light and nutrients, independent of the pycnocline. Our data suggest that it maintains its position not through buoyancy regulation, but primarily through continuous new production that outpaces continuous losses.

A seasonal analysis of historical data indicates that the Chl *a* maximum is shallowest in May, deepening to an average of \sim 30 m by June, where it stagnates for 3 months. SCM development on the Chukchi shelf now appears to be inextricably tied to under-ice blooms: our data suggest that surface blooms begin under the ice pack \sim 1 month before sea ice retreat, and have already reached the subsurface at \sim 15 m by the time ice finally retreats, beyond the visibility of satellite ocean color sensors. This may lead satellite-based approaches to drastically underestimate annual NPP on the Chukchi shelf.

The maximum depth of the SCM on the pan-Arctic continental shelves appears constrained to \sim 30 m by limited light penetration through these optically thick surface waters with relatively high concentrations of CDOM and Chl *a*, which play roughly equal roles

in attenuating light. This may have profound consequences for total Arctic NPP, as the large stores of NO_3^- on Arctic shelves residing deeper than 30 m are unlikely to be utilized during the growth season. These data support the hypothesis of Palmer et al. (2013) that primary productivity on Arctic shelves is controlled by the dynamic balance between light and nutrient availability, being primarily N-limited in surface waters and light-limited at depth.

The SCM was not co-located with the NPP maximum during our study in June–July, being significantly deeper by \sim 16 m. Nevertheless, simulated in situ incubations showed that the SCM is an actively growing community during this time, with a new production rate of \sim 33 mg C m⁻³ d⁻¹, consistent with its ability to maintain its optimal position in the water column.

The productivity and seasonal dynamics of the SCM appear fundamentally different on the Chukchi shelf compared to the Beaufort Sea and CAA, where previous in-depth studies of the SCM have been undertaken. This is almost certainly due to the perennial stratification of the Beaufort Sea and CAA, limiting $NO_3^$ renewal in surface waters. In the future, additional heat and freshwater stratification may push the Chukchi and other Arctic shelves toward productivity regimes similar to those of the stratified waters of the Canadian Arctic, thus increasing the relative importance of the SCM.

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