Optical impact of an Emiliania huxleyi bloom in the frontal region of the Barents Sea

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1. Introduction

The coccolithophorid *Emiliania huxleyi* (Lohmann) Hay and Mohler is a cosmopolitan species, and an important contributor to pelagic calcite formation through the production of calcareous platelets called coccoliths (Paasche, 2001; Thierstein and Young, 2004). In the post-exponential growth phase, the alga produces large amounts of coccoliths, which are roughly 0.7–1.2 μm in size, shedding the surplus leaves through the sea surface to the light incident on it, and c), as a consequence of this the term "bloom" is somewhat unclear, as this species normally constitutes less than 50% of the phytoplankton biomass even at cell concentrations of $10^{10}$ m$^{-3}$ (Paasche, 2012, doi:10.1016/j.jmarsys.2012.07.002). The behavior of light in coccolith-laden waters occurring in the open ocean is mainly governed by the additive effects of absorption by sea water and *chromophoric dissolved organic matter* (CDOM), scattering and absorption by phytoplankton represented by the Chl a concentration, and scattering by coccoliths (Kirke, 1994).

Scattering by coccoliths has a profound effect on the optical properties of underwater and water-leaving light by: a) increasing the mean angle of downwelling light away from zenith, which in turn increases the probability that a photon will be absorbed in the near surface, b) increasing the reflectance, $R$, which is the ratio of light that leaves through the sea surface to the light incident on it, and c), as a result of a) and b), the spectral attenuation coefficient for diffuse downwelling light, $K_{a}(X)$, will increase (Kirke, 1994). With coccoliths present, scalar light radiation is intensified in the upper part of the sea, while reduced at depth (Tyrrell et al., 1999). This scavenging of light may limit photosynthetic production at depths with otherwise sufficient nutrient levels.

Blooms of *E. huxleyi* occur globally except for the Arctic Basin and high latitude Southern Ocean (Winter and Siesser, 1994). However, the term 'bloom' when associated with *E. huxleyi* is somewhat unclear, as this species normally constitutes less than 50% of the phytoplankton biomass even at cell concentrations of $10^{10}$ m$^{-3}$ (Paasche, 2012, doi:10.1016/j.jmarsys.2012.07.002).
In the literature, a ‘bloom’ of *Emiliania huxleyi* is seldom defined, but is commonly understood as concentrations > 10^9 cells m^-3 (Holligan et al., 1983; Tyrrell and Merico, 2004; Tyrrell et al., 1999). This threshold is largely based on the assumption of a correlation between satellite-derived calcite estimates and cell numbers. However, that basis is often misleading because of the bloom dynamics of *E. huxleyi*: the ratio of calcification to photosynthesis increases when the cell concentration begins to decline. As the shed coccoliths are only slowly dissolved in the upper 4–5 km of the ocean, above the calcite lysoclone (Broecker and Peng, 1982), they accumulate in suspension while the cell numbers are in fact decreasing (Buitenhuis et al., 2001; Fernández et al., 1993; Holligan et al., 1993; Volent et al., 2011).

In this paper, we refer to ‘blooms’ of *E. huxleyi* as the extent of the coccolith-laden waters with a temporary (typically 3–4 months) increase in calcite concentrations to above 36 mg PIC m^-3 (Gordon and Balch, 1999). During *E. huxleyi* bloom peaks in the Barents Sea, coccoliths in conspicuous amounts easily cover >250,000 km^2 after 5–7 weeks of development, whereupon the standing stock of PIC in the region may reach 0.8 Tg calcite C, indicating a significant impact on the carbon flux (unpubl. data). The global average PIC concentration from the MODIS Aqua mission data set, years 2002–2011, indicates that the pelagic production of PIC is highest in Sub-Arctic and Polar Regions and especially high in the Barents Sea (Fig. 1). Note that the high values on the Siberian shelf are most likely due to riverine input, as coccolithophorid blooms have never been recorded in Arctic waters before. Coincidently, the Sub-Arctic region of the Atlantic is an important CO₂ sink and simultaneously most sensitive to ocean acidification, which enhances calcite solubility (Feely et al., 2004; Takahashi et al., 2005). In this context, studies of *E. huxleyi* in the Barents Sea are important as the occurrence and success (or prospective decline) of this calcifying species is likely to be affected by anthropogenic carbon emission and climate change (Balch and Utgoff, 2009; Iglesias-Rodríguez et al., 2008; Riebesell, 2004, and others).

The abundance of *E. huxleyi* in the Barents Sea is tightly linked with the dynamics of Atlantic water masses (Hovland, 2007; Pettersen et al., 2011). In our study we utilized the Polar Front in the northern Barents Sea as a natural laboratory where the Arctic side north of the Front was more or less free of coccoliths while transiting to the Atlantic side represented a steep gradient of increased optical impact by *E. huxleyi* coccoliths. By modeling the effect on irradiance of all other known important optical components (water, CDOM and phytoplankton), the effect of the coccoliths on the light field can be quantified. With this intent, investigations were performed starting in Arctic Water (ArW) on Storbanken (Great Bank) and crossing through frontal mixed water (FMW) to the coccolith-laden Atlantic Water (AW) in the Hopen Trench. Additionally, measurements were taken in ArW on Spitsbergenbanken (Spitsbergen Bank). Together, all stations constitute what will simply be referred to as the ‘transect’ in this paper.

We present spectral data on *K_\text{a*}, underwater downwelling irradiance (\text{E}_d), R*, phytoplankton light absorption and CDOM as well as chlorophyll a (Chl a) concentrations measured along the transect. We introduce a method of estimating coccolith PIC concentrations, based on calculating backscattering from irradiance depth profiles, and compare our results to satellite data. Subsequently, we use the calculated PIC in conjunction with the measured optical parameters as input to Ecolight (Sequoia Scientific, Inc.) in order to model the light field along the transect. The model output is used to examine the impact of phytoplankton, CDOM and PIC on \text{E}_d and the photosynthetically usable radiation (\text{PUR}) in the Frontal Region of the central Barents Sea. We also discuss how this affected the potential for primary production (\text{PP}_\text{pot}) in the study area.

2. Material and methods

2.1. Study area

As part of the International Polar Year (IPY) project NESSAR (Norwegian Ecosystem Study of Subarctic and Arctic Regions), an interdisciplinary cruise was conducted in the Barents Sea with the R/V *Jan Mayen* from 1 to 16 August 2007 to investigate the Polar...
Front dynamics and their effect on productivity and distribution of marine organisms. As part of this study, bio-optical measurements including profiles of irradiance from which we were able to investigate the impact of *E. huxleyi* coccoliths on the downwelling irradiance spectrum, $E_d(\lambda)$ (Table 1). 12 full bio-optical stations, which in this paper is used to denote stations with measured Chl a or CDOM profiles, were occupied on Spitsbergenbanken, Storbanken and the Hopen Trench, (Fig. 2A). Bottom depths varied from over 300 m in the Trench to 78 m and 107 m on the top of Spitsbergenbanken and Storbanken, respectively. In addition to the full stations, another 12 supplementary stations with only CTD (conductivity, temperature and depth) and $E_d$ profiles were visited to enhance the resolution of the transect. Note that the optical measurements were not taken regularly (i.e. in sequence) along the transect (Table 2). Several other CTD stations were taken as part of hydrographic surveys of the region during the cruise and used herein to better define the physical oceanography of the region, as well as for *E. huxleyi* enumeration.

### 2.2. Bio-optical water sampling and analyses

During the cruise, depth profiles of salinity and temperature were measured with a Sea Bird Electronics (SBE) CTD SBE911+ package equipped with a fluorometer (Aqua-3L) attached to a SBE32 rosette equipped with 12 5-liter Niskin bottles for water sampling. Surface water samples were collected with a clean plastic bucket lowered over the side. Samples for calibrating salinity were taken routinely that the optical measurements were not taken regularly (i.e. in sequence) along the transect (Table 2). Several other CTD stations were taken as part of hydrographic surveys of the region during the cruise and used herein to better define the physical oceanography of the region, as well as for *E. huxleyi* enumeration.

#### Table 1

Selected abbreviations and units used in this paper. Radiometric quantities are gathered at the end and can be considered as spectral quantities when the argument $\lambda$ (wavelength) is added.

<table>
<thead>
<tr>
<th>Abbreviation</th>
<th>Unit</th>
</tr>
</thead>
<tbody>
<tr>
<td>Arctic Water</td>
<td>AW</td>
</tr>
<tr>
<td>Atlantic Water</td>
<td>AW</td>
</tr>
<tr>
<td>Barents Sea</td>
<td>BS</td>
</tr>
<tr>
<td>Chlorophyll a</td>
<td>$\text{mg} \text{m}^{-3}$</td>
</tr>
<tr>
<td>Chl a absorption coefficient</td>
<td>$a_{\text{opt}}$ $\text{m}^{-1}$  $(\text{mg Chl a})^{-1}$</td>
</tr>
<tr>
<td>Chromophoric dissolved organic matter</td>
<td>$a_{\text{abs,CDOM}}$ $\text{m}^{-1}$</td>
</tr>
<tr>
<td>CDOM concentration</td>
<td>$a_{\text{abs,CDOM}}$ $\text{m}^{-1}$</td>
</tr>
<tr>
<td>Euphotic zone (1% light depth)</td>
<td>$w_{	ext{eup}}$ m</td>
</tr>
<tr>
<td>Euphotic zone midpoint (10% light depth)</td>
<td>$z_{10}$ m</td>
</tr>
<tr>
<td>Frontal mixed water</td>
<td>FMW</td>
</tr>
<tr>
<td>Optically homogeneous surface layer</td>
<td>OHSIL</td>
</tr>
<tr>
<td>Particulate inorganic matter</td>
<td>PIC</td>
</tr>
<tr>
<td>From satellite imagery</td>
<td>PICsat $\text{mg} \text{C}^{-1}$</td>
</tr>
<tr>
<td>From $b_{\text{b}}$ estimates</td>
<td>PICb $\text{mg} \text{C}^{-1}$</td>
</tr>
<tr>
<td>Photometrically active radiation (from 400 to 700 nm wavelength)</td>
<td>PAR $\text{mol photons m}^{-2} \text{s}^{-1}$</td>
</tr>
<tr>
<td>Photosynthetically usable radiation (fraction of $E_d$ absorbed by algae)</td>
<td>PUR $\text{mol photons}$</td>
</tr>
<tr>
<td>Potential primary production</td>
<td>$PP_{\text{pot}}$ $\text{PP mol C d}^{-1}$</td>
</tr>
<tr>
<td>Absorption coefficient</td>
<td>$a$ $\text{m}^{-1}$</td>
</tr>
<tr>
<td>Scattering coefficient</td>
<td>$b$ $\text{m}^{-1}$</td>
</tr>
<tr>
<td>Backscattering coefficient</td>
<td>$b_{\text{h}}$ $\text{m}^{-1}$</td>
</tr>
<tr>
<td>Irradiance</td>
<td>$E_d$ $\text{mol photons m}^{-2} \text{s}^{-1}$</td>
</tr>
<tr>
<td>Downwelling</td>
<td>$E_d$ $\text{mol photons m}^{-2} \text{s}^{-1}$</td>
</tr>
<tr>
<td>Upwelling</td>
<td>$E_u$ $\text{mol photons m}^{-2} \text{s}^{-1}$</td>
</tr>
<tr>
<td>Reflectance</td>
<td>$R = E_d / E_u$</td>
</tr>
<tr>
<td>Vertical diffuse light attenuation coefficient</td>
<td>$K$ $\text{m}^{-1}$</td>
</tr>
<tr>
<td>Downwelling</td>
<td>$K_d$ $\text{m}^{-1}$</td>
</tr>
<tr>
<td>Upwelling</td>
<td>$K_u$ $\text{m}^{-1}$</td>
</tr>
</tbody>
</table>

Water samples of 263 mL for Chl a and degraded Chl a (e.g. phaeophorbide a and phaeophytin a) quantification were taken from the Niskin bottles triggered at various depths ranging from near surface to 250 m and passed through Whatman GF/C glass fiber filters as part of the standard sampling procedure of the IMR. The pigments were quantified fluorometrically at IMR following extraction in 90% acetone after the method of Holm-Hansen et al. (1965).

The phytoplankton in vivo spectral absorption coefficient normalized to Chl a [$\varphi_{\text{ph}}(\lambda)$], expressed in units of $\text{m}^{2} \text{mg} \text{Chl a}^{-1}$, was measured using the ‘Filter Pad Technique’ (Mitchell and Kiefer, 1988; Yentsch, 1962). Particulate absorption was calculated from sea water ($0.8–2$ L) passed through glass fiber filters (Whatman GF/F, 0.4 $\mu$m) and the phytoplankton absorption obtained after correction for the non-algal particulate absorption by bleaching the filters in methanol for 3 h, using the protocol suggested by Mitchell et al. (2002). Filters were kept in liquid nitrogen until analyses were performed within 3 months after sampling. Absorbance was measured from triplicate samples in a dual-beam spectrophotometer (Hitachi 150-20) from 350 to 800 nm at 1 nm increments. Correction for path length amplification was made according to Mitchell (1990) using parameters recommended for naturally mixed phytoplankton communities by Cleveland and Weidemann (1993). Water samples (50 mL) for CDOM measurements were frozen ($-20^\circ$C) within an hour after filtration (0.2 $\mu$m sterile syringe filter). CDOM absorption was quantified spectrophotometrically approximately 3 months after sampling (for details, see Hancke et al., this issue).

#### 2.3. Light measurements

Measurements of spectral irradiance (in $\text{mol photons m}^{-2} \text{s}^{-1} \lambda^{-1}$) were performed with a Ramses ACC-VIS Spectroradiometer (TriOS GmbH, 350–900 nm range at 3.3 nm resolution) attached to the CTD winch. The radiometer was lowered −5 m from the ship using a crane in order to avoid sunlight reflection and any shadow effects. The sensor was mounted in a metal frame facing upwards to measure $E_d(\lambda)$ and subsequently, within 8 min, mounted facing downwards in order to measure upwelling irradiance [$E_u(\lambda)$] on a separate second run. Measurements were taken at 1 m increments from 0 to 10 m, and then at 12 and 15 m followed by 10 m increments from 20 m and downwards, until the total $E_u$ in the full range was less than 1 $\text{mol m}^{-2} \text{s}^{-1}$. Incident spectral irradiance was measured while the sensor was hanging in the air, before the underwater $E_d$ cast.

#### 2.4. Satellite data

In order to obtain estimates of PIC, in units $\text{mg C m}^{-3}$, from satellite imagery, PICsat, a level-3 averaged PIC image for August 1–16 was generated from all available level-2 scenes of the PIC product from MODIS Aqua (Fig. 2B), downloaded from OceanColorWeb (http://oceancolor.gsfc.nasa.gov/). This was done via the level-3 product generator in BEAM (Brockmann Consulting Ltd.). PICsat was exported as i) a mean of 3 × 3 pixels surrounding each full station for direct comparison with PICobs from these stations, and ii) a continuous line of PIC values along the transect.

### 3. Calculations

#### 3.1. Calculation of light attenuation and reflectance

Measurements from the optically homogeneous surface layer (OHSIL), determined for each station as the depth of the upper layer...
of constant attenuation of light, were used for calculation of the diffuse attenuation coefficients ($k$, subscript $d$ for downwelling and $u$ for upwelling):

$$K_d(\lambda) = \frac{1}{E_d(\lambda)} \frac{dE_d(\lambda)}{dz}$$  \hspace{1cm} (1)

and

$$K_u(\lambda) = \frac{1}{E_u(\lambda)} \frac{dE_u(\lambda)}{dz}$$  \hspace{1cm} (2)

where $z$ is depth in meters and $\lambda$ is the wavelength. Immediate subsurface values $E_{d,0}(\lambda)$ and $E_{u,0}(\lambda)$ were extrapolated from the light measurements using the $K(\lambda)$ value for $E_{d,0}(\lambda)$ and $K_u(\lambda)$ for $E_{u,0}(\lambda)$ calculated over the OHSL depth. Subsurface irradiance reflectance ($R$) was calculated as:

$$R(\lambda) = \frac{E_{u,0}(\lambda)}{E_{d,0}(\lambda)}$$  \hspace{1cm} (3)

for each station (Kirk, 1994).

### Table 2

List of stations with their respective parameters used for modeling the light field, sorted by increasing $PIC_{b}$: Explanation: Station is the CTD number. Water types denote whether the station was situated in ArW, FMW or AW. Date is day in August 2007. $PIC_{b}$ refers to the PIC concentration used in the model, reaching from the surface to the depth given in column OHSL (optically homogenous surface layer). $Cc$ is the ship-observed percentage of cloud cover, at the time of taking the $E_d(\lambda)$ profile.

<table>
<thead>
<tr>
<th>Station (Nr.)</th>
<th>Latitude (°N)</th>
<th>Longitude (°E)</th>
<th>Water type</th>
<th>Date (day)</th>
<th>Time (hh:mm)</th>
<th>$PIC_{b}$ (mg C m⁻³)</th>
<th>OHSL (m)</th>
<th>Wind (m/s)</th>
<th>$Cc$ (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>213</td>
<td>76.5341</td>
<td>26.4885</td>
<td>ArW</td>
<td>3</td>
<td>11:12</td>
<td>8</td>
<td>45.0</td>
<td>6.0</td>
<td>100</td>
</tr>
<tr>
<td>316</td>
<td>76.5380</td>
<td>32.7670</td>
<td>FMW</td>
<td>15</td>
<td>04:54</td>
<td>12</td>
<td>3.5</td>
<td>5.5</td>
<td>75</td>
</tr>
<tr>
<td>304</td>
<td>76.6319</td>
<td>32.9571</td>
<td>FMW</td>
<td>12</td>
<td>11:59</td>
<td>15</td>
<td>3.4</td>
<td>2.0</td>
<td>75</td>
</tr>
<tr>
<td>282</td>
<td>76.8390</td>
<td>33.8120</td>
<td>ArW</td>
<td>11</td>
<td>10:53</td>
<td>18</td>
<td>3.8</td>
<td>7.5</td>
<td>63</td>
</tr>
<tr>
<td>317</td>
<td>76.5380</td>
<td>32.5170</td>
<td>FMW</td>
<td>15</td>
<td>09:24</td>
<td>21</td>
<td>17.5</td>
<td>8.0</td>
<td>50</td>
</tr>
<tr>
<td>223</td>
<td>76.8168</td>
<td>29.3066</td>
<td>AW</td>
<td>6</td>
<td>20:05</td>
<td>23</td>
<td>20.0</td>
<td>6.0</td>
<td>63</td>
</tr>
<tr>
<td>254</td>
<td>76.5903</td>
<td>32.7436</td>
<td>FMW</td>
<td>10</td>
<td>16:23</td>
<td>32</td>
<td>25.0</td>
<td>6.0</td>
<td>63</td>
</tr>
<tr>
<td>199</td>
<td>76.0051</td>
<td>30.0204</td>
<td>AW</td>
<td>1</td>
<td>12:59</td>
<td>49</td>
<td>27.5</td>
<td>9.0</td>
<td>100</td>
</tr>
<tr>
<td>236</td>
<td>76.1420</td>
<td>31.6647</td>
<td>AW</td>
<td>9</td>
<td>05:31</td>
<td>68</td>
<td>30.0</td>
<td>8.0</td>
<td>100</td>
</tr>
<tr>
<td>238</td>
<td>76.3455</td>
<td>31.8014</td>
<td>AW</td>
<td>9</td>
<td>11:13</td>
<td>99</td>
<td>30.0</td>
<td>6.2</td>
<td>95</td>
</tr>
<tr>
<td>234</td>
<td>76.2374</td>
<td>31.2482</td>
<td>AW</td>
<td>8</td>
<td>06:36</td>
<td>120</td>
<td>30.0</td>
<td>3.0</td>
<td>100</td>
</tr>
<tr>
<td>232</td>
<td>76.2515</td>
<td>29.9834</td>
<td>AW</td>
<td>8</td>
<td>03:53</td>
<td>133</td>
<td>20.0</td>
<td>5.0</td>
<td>100</td>
</tr>
</tbody>
</table>

### 3.2. PIC estimates from backscattering

Total backscattering, $b_b(\lambda)$, was calculated from $K_d(\lambda)$ and $R(\lambda)$; formulated by Gordon et al. (1988) and reviewed by Gordon (2002):

$$b_b(\lambda) \approx \frac{K_d(\lambda)}{R(\lambda)} \frac{R(\lambda)}{k}$$  \hspace{1cm} (4)

where $k$ is an empirical variable equal to 0.35 for a totally diffuse radiance distribution. Under natural circumstances in relatively clear water, where radiance is partially directional, $k$ will range from 0.44 to 0.55 (Gordon et al., 1988). We chose to use $k = 0.35$ because heavily coccolith-laden waters are more optically diffuse than clear waters.

For our purposes, $b_b$ can be decomposed as follows:

$$b_b(\lambda) = b_{bw}(\lambda) + b_{Chl}(\lambda) + b_{bPIC}(\lambda)$$  \hspace{1cm} (5)

where $b_{bw}$ is backscattering for pure, natural seawater (Kirk, 1994), $b_{Chl}$ is backscattering from phytoplankton based on Chl $\alpha$ concentrations (Loisel and Morel, 1998) and $b_{bPIC}$ is the coccolith-specific backscattering. From Eq. (5), we calculated $b_{bPIC}(\lambda)$ accordingly:

$$b_{bPIC}(\lambda) = b_b(\lambda) - b_{bw}(\lambda) - b_{Chl}(\lambda).$$  \hspace{1cm} (6)

PIC concentrations for each station were calculated using the following relation of coccolith-specific backscattering to PIC (Ackleson et al., 1994; Tyrrell et al., 1999):

$$PIC_{b} = b_{bPIC}(\lambda)/4.54\lambda_{rf}^{-1.4}$$  \hspace{1cm} (7)

where $\lambda_{rf}$ is any chosen reference wavelength (here, 485 nm), $PIC_{b}$ is the concentration of coccolith-bound calcite carbon, in units of mg bicarbonate-C m⁻³, and $\lambda_{rf}^{-1.4}$ describes the shape of coccolith backscattering as a function of wavelength (Voss et al., 1998). This shape was chosen to replace the original $\lambda_{rf}^{-1.45}$ from Ackleson et al. (1994) because those authors themselves questioned its validity. We chose $\lambda_{rf} = 485$ nm due to the shape of the $b_b$ spectra as discussed in Section 5.3, and to minimize influence on scattering by phytoplankton cells.
4. Light modeling

4.1. Model description

Ecoilight is a module within the Hydrolight software, which contains a radiative transfer model that provides a quantitative description of most important aspects of the underwater light field (Mobley, 1989; Mobley and Sundman, 2008). The model is based on user input of the absorption and scattering properties normalized to concentration of the different components, as well as profiles of the components themselves. Our chosen sub-model concerned case-2 waters (Morel and Prieur, 1977) and comprised four optical components, namely 1) pure sea water, 2) phytoplankton, 3) CDOM and 4) coccolith PIC, all described in the next 4 sections. The model output was set to 20 nm bands from 350 to 700 nm. This bandwidth was chosen to keep computation loads suitably low for future implementation to spectrally resolved ecosystem models. The vertical resolution was set to 1 m over the upper 50 m, with an infinitely deep optical water column (no bottom reflectance).

Transmission of light through the sea surface was computed by Hydrolight using field measured, sea surface incident $E(\lambda)$ in conjunction with wind and cloud cover data from the ship log as parameters, for all 12 stations except 238. For 238, the measured incident $E(\lambda)$ was compromised by water on the sensor (data not shown) so instead, incident $E(\lambda)$ for station 238 was calculated by Hydrolight using the built-in RADTRAN model for direct and indirect sunlight as described by Mobley and Sundman (2008). The local CDOM profile was incorporated into the model as depth dependent (S.R. Erga, pers. comm.).

The model was run for all 12 stations in order to examine the agreement with the measured, sea surface incident $E(\lambda)$ from station 234 for all other stations. Chl$\alpha$ concentration profiles were scaled relative to these. This provided a means of separating the relative impact of PIC, phytoplankton and CDOM on $E_d$ for each station independently of the calculated $E_d$ for the surface.

4.2. Component 1: pure seawater

The spectral absorption and scattering of light by seawater itself was taken from Smith and Baker (1981), as embedded in the Ecoilight software.

4.3. Component 2: phytoplankton

Spectral absorption by phytoplankton normalized to Chl$\alpha$ was entered into the model using the local $a_{ap}^{\text{Fl}}(\lambda)$ for station 238 and the general $a_{ap}^{\text{Fl}}(\lambda)$ from station 234 for all other stations. Chl$\alpha$-specific scattering was modeled by the near-surface equation from Loisel and Morel (1998), as embedded in the software model. The ratio of backscattering to scattering ($b_b:b$) for Chl$\alpha$ was set to 0.005 (David et al., 2011).

For each station except 213, local depth profiles of Chl$\alpha$ concentrations were used. For station 213 Chl$\alpha$ was not measured, and the profile from station 282 was used as it was the only other full, Arctic station. The depths where irradiance was 1% of subsurface values (termed the “eutrophic zone”, $z_{eu}$) were separated by 2.2 m between 213 and 282, indicating similar attenuation properties, and glider data showed a layer of subsurface maximal fluorescence at both stations (S.R. Erga, pers. comm.).

4.4. Component 3: CDOM

Measured spectral absorption of CDOM ($a_{cdom}$, m$^{-1}$) at a reference wavelength (350 nm) and a single mean slope coefficient (S) was incorporated into the model as depth profiles. CDOM is assumed to be non-scattering by the model (Mobley and Sundman, 2008). The local CDOM profile for each station was applied when present, otherwise the profile from the closest station was substituted. Thus, for stations 232, 236, 316 and 317 the CDOM profiles from 234, 238, 304 and 304 were used, respectively. For station 213 the profile of 282 was used for the same reason stated in Section 4.3. This should not introduce large errors, as the average [± standard deviation (S.D.)] $a_{cdom}(350)$ was 0.19 ± 0.07 m$^{-1}$ for the entire cruise (Hancke et al., this issue).

4.5. Component 4: PIC

Only coccolith PIC was considered in our model and absorption for this component was set to zero as this mineral form is considered to have negligible light absorption properties (Mobley, 1994). The spectral scattering coefficients per unit of PIC were taken from a study in the Gulf of Maine described by Balch et al. (1991). The ratio $b_b:b$ for PIC was set to 0.043 (Ackleson et al., 1994), also from the Gulf of Maine.

PIC concentration profiles for each station were created by taking $PIC_{lab}$ calculated from Eq. (7) for the surface and extrapolating that value to the OHSL depth (Table 2). Below that depth, we assumed a low impact of PIC and, accordingly, reduced PIC to a negligible concentration of 0.001 g m$^{-3}$ for a transition layer of 3 m in the profile.

4.6. Impact on $E_d$ of phytoplankton, CDOM and PIC

The $E_d(\lambda)$ profiles measured in the field represented the total optical impact of phytoplankton, CDOM and PIC. By modeling the spectrum of $E_d$ with only CDOM and Chl$\alpha$ present, the impact of PIC on the downwelling light field can be estimated by subtracting the measured $E_d$ spectrum. We chose the three stations (232, 234 and 238) with the highest estimated $PIC_{lab}$ values and the best $E_d(\lambda)$ profile agreement for this. The measured $E_d$ spectra at the 10% irradiance depth, $z_{10}$, were normalized to 1 at their peak wavelength and the modeled spectra were scaled relative to these. This provided a means of separating the relative impact of PIC, phytoplankton and CDOM on $E_d$, independently of the calculated $PIC_{lab}$. As station 232 was affected by changing skylight conditions below 13 m during the profiling we used the model data to calculate $z_{eu}$ for this particular station. This value was not used in evaluation of the model. $z_{eu}$ is the depth where $E_d(\lambda)$ is 95% of $E_d(\lambda)$ just below the surface.

4.7. Impact on potential primary production

Photosynthetically usable radiation (PUR) is the fraction of radiation that can be used by phytoplankton to drive photosynthesis (Morel, 1978; Sakshaug et al., 1997). After normalizing the measured $E_d(\lambda)$ spectra at $z_{10}$ to an equal area of 1, PUR could be calculated as:

$$PUR = \frac{\int_{400}^{700} E_d(\lambda) \cdot a_{ap}(\lambda) \cdot a_{cdom}(\lambda) \cdot a_{fl}(\lambda)}{\int_{400}^{700} E_d(\lambda) \cdot a_{ap}(\lambda).}$$

In order to estimate the relative potential for primary production ($PP_{pot}$) in the different water types, we contrived a simplified model using PUR while taking into account the measured, subsurface normalized $E_d$(PAR) and Chl$\alpha$ as a function of depth. $PP_{pot}$ at each full station was calculated thus:

$$PP_{pot} = \int_{0}^{50} PUR \cdot Chl(z) \cdot E_d(\lambda)dz.$$

In the $PP_{pot}$ model, all Chl$\alpha$ represented productive phytoplankton down to 50 m. Physical and physiological effects such as nutrient limitation and pigment acclimation states are assumed proportional to
5. Results and discussion

5.1. Hydrographic description of the investigation area

The study area (Fig. 2) contained two main water masses, Atlantic Water that was primarily confined within the Hopen Trench and Arctic Water that covered most of Spitsbergenbanken and Storbanken. These water masses were separated by the Polar Front which exhibited relatively strong horizontal gradients in temperature and salinity but weak density gradients because of density compensation (Fer and Drinkwater, this issue; Våge et al., this issue). As *Emiliania huxleyi* is primarily found in the top 100 m of the water column, we focus our discussion of the hydrographic properties in this depth range. Arctic Water temperatures during August of 2007 varied from 3° to 6.5 °C with salinities near or above 35 (Fig. 3), consistent with earlier studies of the hydrographic properties in this depth range. Atlantic Water temperatures presented a clear difference between the two banks: Arctic Water (ArW) off Storbanken had temperatures ranging from ~1° to 6 °C and salinities between 34.4 and 34.8 (Fig. 3A). The highest temperatures were caused by solar heating of the UML. On the shallow, ArW-dominated part of Spitsbergenbanken maximum temperatures only reached 3 °C and salinities were fresher, as low as 34 (Fig. 3B). This difference in Arctic Water properties between the two banks arose because of the spatial difference in the formation processes (Loeng, 1991). Temperature and salinity properties in the frontal region lay intermediate between the two water masses (Fig. 3), hence we have labeled them as *frontal mixed water* (FMW). Both the Chl *a* and the *Emiliania huxleyi* abundance in FMW were more similar to ArW than AW. The Chl *a* and cell concentrations were comparable to studies of *Emiliania huxleyi* blooms in the North Atlantic and the North Sea: The North Sea study observed ~0.3·10⁹ E. *huxleyi* cells m⁻³ and ~0.7·1.2 mg Chl *a* m⁻³ at two stations with 75 and 150 mg PIC m⁻³ (Van der Wal et al., 1995). The North Atlantic study observed ~0.4·4·10⁹ E. *huxleyi* cells m⁻³ and ~0.8·3·10⁹ Chl *a* m⁻³ at three stations with ~30·200 mg PIC m⁻³ (Fernández et al., 1993). If there is a correlation between *Emiliania huxleyi* and coccolith concentration, we would from the cell counts expect the highest *Kₚ* around 30 and 31°E. However, the highest *Kₚ* values were observed from 31 to 32°E (Fig. 6), and the cell counts from 38 discrete depths from 7 stations showed an average of 30·10⁶ cells m⁻³ and 28 samples with no *Emiliania huxleyi* cells. The lack of correlation between cells and coccoliths is explained by the accumulation of coccoliths while *Emiliania huxleyi* is declining, as explained in Section 1, which is important when attempting to relate satellite images of PIC to biological activity.

5.2. Biological variation along the transect

Surface (0–3 m) Chl *a* concentrations were generally low (~0.1–0.5 mg m⁻³) in FMW and the Arctic side of the Polar Front towards both Storbanken and Spitsbergenbanken while higher (~1–2 mg m⁻³) in AW. A subsurface Chl *a* maximum of ~1 mg Chl *a* m⁻³ was observed near 30 m at ArW station 282 (Fig. 4). The fluorescence maximum on Storbanken coincided with the pycnocline (Våge, 2010), and glider data showed that this phenomenon was a prominent feature of ArW on Spitsbergenbanken as well (S.R. Erga, pers. comm.). In ArW, only 2 out of 24 samples, stations 282 and 207 (5 nm NE of 213), contained *Emiliania huxleyi* cells, with 0.5·10⁶ and 1·10⁶ cells m⁻³ at the surface (Table 3). Similarly, only 2 out of 27 samples from FMW contained *E. huxleyi* cells; 0.5·10⁶ cells m⁻³ for station 310 (5.7 nm SW of 317, depth 20 m) and 20·10⁶ cells m⁻³ for station 254 (at surface). In AW, *E. huxleyi* was more common, but with a patchy distribution. Here, 14 of the 52 samples (from 7 out of 12 CTD casts along the Atlantic part of the transect) contained identifiable *E. huxleyi* cells (Fig. 5). Two samples displayed concentrations above 10⁹ cells m⁻³ and these were taken around 30°E at station 199 (depths 5 and 10 m). There was also a notable concentration of 0.8·10⁹ cells m⁻³ around 31° E, at station 234 (depth 20 m). While these results must be interpreted with caution due to the age of the phytoplankton samples, they do support that *E. huxleyi* is rarely found in ArW (Pettersen et al., 2011; Winter and Siesser, 1994). Both the Chl *a* and the *E. huxleyi* abundance in FMW were more similar to ArW than AW. The Chl *a* and cell concentrations were comparable to studies of *E. huxleyi* blooms in the North Atlantic and the North Sea: The North Sea study observed ~0.3·1·10⁹ E. *huxleyi* cells m⁻³ and ~0.7·1·2 mg Chl *a* m⁻³ at two stations with 75 and 150 mg PIC m⁻³ (Van der Wal et al., 1995). The North Atlantic study observed ~0.4·4·10⁹ E. *huxleyi* cells m⁻³ and ~0.8·3·10⁹ Chl *a* m⁻³ at three stations with ~30·200 mg PIC m⁻³ (Fernández et al., 1993). If there is a correlation between *Emiliania huxleyi* and coccolith concentration, we would from the cell counts expect the highest *Kₚ* around 30 and 31°E. However, the highest *Kₚ* values were observed from 31 to 32°E (Fig. 6), and the cell counts from 38 discrete depths from 7 stations showed an average of 30·10⁶ cells m⁻³ and 28 samples with no *Emiliania huxleyi* cells. The lack of correlation between cells and coccoliths is explained by the accumulation of coccoliths while *E. huxleyi* is declining, as explained in Section 1, which is important when attempting to relate satellite images of PIC to biological activity.

5.3. Optical properties along the transect

Coccoliths had a dramatic effect on the color of the sea, turning it from clear, dark blue in the Arctic Water to turbid and green in the

![Fig. 3. Potential temperature vs. salinity plots for stations at A: Storbanken and B: Spitsbergenbanken. Color version is available online.](Image)
Atlantic coccolith-laden part of the transect, as shown in Fig. 6, panels B and C. The diffuse attenuation of photosynthetic available radiation \([K_d(\text{PAR}), 400–700 \, \text{nm}]\) over the upper 30 m increased from <0.1 in the Arctic waters to 0.15–0.35 m\(^{-1}\) in the Atlantic waters. A one-way ANOVA test comprising all 24 \(E_d(\text{PAR})\) profiles showed

Table 3
Biological variables measured in the transect: cell counts and Chl \(a\) concentrations averaged for each water type. The sample total is the number of water samples investigated for presence of \(E. \text{huxleyi}\) cells. \(n_{\text{samples}}\) is the number of samples that contained \(E. \text{huxleyi}\) and the mean and S.D. are given for these. \(n_{\text{chl}}\) is the number of full stations with data on Chl \(a\) concentrations per square meter.

<table>
<thead>
<tr>
<th>Sample (type)</th>
<th>Sample total (#)</th>
<th>(n_{\text{samples}}) (#)</th>
<th>Mean (10(^6) cells (\text{m}^{-3}))</th>
<th>S.D. (\pm 10(^6) cells (\text{m}^{-3}))</th>
<th>(n_{\text{chl}}) (#)</th>
<th>Chl (a) (mg (\text{m}^{-2}))</th>
</tr>
</thead>
<tbody>
<tr>
<td>ArW</td>
<td>24</td>
<td>2</td>
<td>5</td>
<td>7</td>
<td>1</td>
<td>22</td>
</tr>
<tr>
<td>FMW</td>
<td>27</td>
<td>2</td>
<td>10</td>
<td>15</td>
<td>4</td>
<td>12</td>
</tr>
<tr>
<td>AW</td>
<td>52</td>
<td>14</td>
<td>350</td>
<td>750</td>
<td>6</td>
<td>34</td>
</tr>
</tbody>
</table>

Fig. 4. Input parameters of optical components: Chl \(a\) (full lines), CDOM (punctured lines) and PIC (dotted lines) as interpolated over depth in the Ecolight model. The stations are sorted from left to right, top to bottom, by increasing PIC values, with their identifiers given in the lower right corner. ArW, FMW and AW denote Arctic, Frontal Mixed and Atlantic Water stations. Color version and source data are available online.

Fig. 5. Distribution of \(E. \text{huxleyi}\) cells along the transect in Atlantic waters, from full stations and supplementary CTD casts. Black filled circles denote zero cells. Gray circles in order of increasing size indicate 1×10\(^6\); 10\(^6\)–10\(^7\); 10\(^7\)–10\(^8\); 10\(^8\)–10\(^9\); 10\(^9\)–10\(^10\); 10\(^10\)–10\(^11\); 10\(^11\)–10\(^12\) and 2×10\(^12\)–3×10\(^12\) cells \(\text{m}^{-3}\). Full station numbers are indicated at the top, with their positions marked by the dotted drop lines. Note that stations 232 and 199 are 15 nm apart (Fig. 2). Source data is available online.

that the depths of the euphotic zones ($z_{eu}$) were significantly different ($P<0.05$) between AW and both ArW and FMW, while ArW and FMW were not. The average $z_{eu}$ was 52 m in ArW, 47 m in FMW and 23 m in AW (Table 4). Thus, the available irradiance for phytoplankton decreased significantly when transiting into Atlantic Water from the Arctic side of the Polar Front.

The irradiance reflectance spectra (Fig. 7) grouped into two different spectral signatures, presumably according to the optical influence of coccoliths: Arctic stations (213 and 282) as well as mixed water stations (254, 304, 316 and 317) and one Atlantic station (223) displayed relatively flat $R$ spectra, while the remaining Atlantic stations (199, 232, 234, 236 and 238) had a marked higher reflectance from 400 to 600 nm. Note that the station with the highest reflectance, 232, displayed relatively few $E. huxleyi$ cells (Fig. 5), while the station where the most $E. huxleyi$ was found, 199, displayed moderate reflectance. This again shows the discrepancy between the living cell distribution and the optical impact of $E. huxleyi$. The peak $R$ of station 223 was at 493 nm, which was between the $R$ peak of ~485 nm in ArW and ~510 nm in AW. In addition, two conspicuous peaks at ~392 nm and ~680 nm, the latter likely from Chl a fluorescence, were visible in the AW $R$ spectra. This is potentially useful for the development of algorithms to separate the water masses by means of remote sensing.

The average coccolith-PIC specific backscattering ($b_{bbPIC}$) at 485 nm was $0.010\, m^{-1}$ at Arctic stations, $0.015\, m^{-1}$ at mixed water stations and $0.065\, m^{-1}$ at Atlantic stations, with an even more pronounced optical grouping than the $R$ spectra (Fig. 8). The theoretical spectral shape of coccolith $b_b$ (that is, $\lambda^{-1.4}$) used in Eq. (7) fitted well to $b_{bbPIC}(\lambda)$ from 400 to 550 nm at all Atlantic stations, and from 400 to 500 nm at all Arctic and mixed water stations except 254 and 282 (Fig. 7). For wavelengths higher than 500 nm, $b_{bbPIC}(\lambda)$ at Arctic stations proportionately increased towards unrealistic values, taking on the apparent shape of $K_b(\lambda)$ by water. In a study by Gordon et al. (2009), both in situ data and models of coccolith scattering showed a relative increase in $b_b(\lambda)$ at high wavelengths, but not of the proportions seen here. This unexpected spectral behavior in $b_b(\lambda)$ above 500 nm is therefore probably an artifact of the $b_{bb}$ theoretical model, with the low underwater light intensities at higher wavelengths resulting in the model to be dominated by the factor $K_b$ in Eq. (4). All in all, we conclude that using $b_b$ at 485 nm as the reference wavelength in Eq. (7) represented physical values in accordance with theory. This is important in modeling PIC concentrations from

Table 4

<table>
<thead>
<tr>
<th>Water type (type)</th>
<th>$n_{data}$ (#)</th>
<th>$z_{eu}$ (m)</th>
<th>Mean $z_{eu}$ (m)</th>
<th>S.D. (±m)</th>
<th>$n_{data}$ (#)</th>
<th>$z_{10}$ (m)</th>
<th>Mean $z_{10}$ (m)</th>
<th>S.D. (±m)</th>
<th>$n_{data}$ (#)</th>
<th>Mean PIC (m$^{-1}$)</th>
<th>S.D. (±m)</th>
</tr>
</thead>
<tbody>
<tr>
<td>ArW</td>
<td>7</td>
<td>52</td>
<td>8</td>
<td>2</td>
<td>2</td>
<td>13</td>
<td>7</td>
<td>6</td>
<td>0.3</td>
<td></td>
<td></td>
</tr>
<tr>
<td>FMW</td>
<td>9</td>
<td>46</td>
<td>5</td>
<td>4</td>
<td>2</td>
<td>20</td>
<td>9</td>
<td>8</td>
<td>5</td>
<td></td>
<td></td>
</tr>
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<td>8</td>
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<td>7</td>
<td>10</td>
<td>2</td>
<td>62</td>
<td>42</td>
<td>77</td>
<td>18</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Fig. 7. Blue, green and red lines show subsurface irradiance reflectance ($R$) spectra calculated from field data at ArW, FMW and AW stations, respectively. Stations are identified in the legend to the right. Color version and source data are available online.
irradiance measurements, but we stress that this conclusion needs further validation.

5.4. Remotely sensed PIC_sat vs. backscattering-based PIC_bb

The relationship between PIC_bb from Eq. (7) and MODIS level-3 PIC_sat from August 1 to 17 for each full station showed a significant linear dependence (P<0.01) with a R^2 of 0.70 (Fig. 9). This corroborates the validity of the PIC_bb calculations. In comparison, a study from several regions obtained R^2 = 0.55 in their relationship between ship derived and remotely sensed PIC (Balch et al., 2005).

In AW, the average PIC_bb was 82 mg C m^{-3}, while remotely sensed PIC_sat was on average 77 mg C m^{-3} (Table 4). For FMW the values for PIC_bb and PIC_sat were 20 and 8 mg C m^{-3}, respectively, while for ArW they were 13 and 6 mg C m^{-3}. This was consistent with the finding that ArW and FMW were optically similar relative to AW, with slightly higher impact of PIC in FMW than ArW. It would seem that PIC_bb is positively biased, which is likely due to the chosen k value of 0.35 (i.e., that the waters were not totally diffuse). The relationship between Kd, R and k given in Eq. (4) has been utilized in optical studies before (e.g., Pelevin and Rostovtseva, 2001), but deemed inapplicable in coccolith-laden waters, where multiple scattering may occur (Balch et al., 1991). However, our results show the potential of this relationship as a simple method for extracting optical properties from sea water even in optically complex waters.

It is unfortunate that we were not able to obtain samples for elemental carbon analysis from the cruise, as discrepancies between PIC_bb and PIC_sat would be expected a priori for three main reasons: First, the satellite overpasses were several days apart from most full stations, which makes the water masses less comparable. Second, coccoliths have a patchy distribution due to surface currents, and a single measurement covers an area several orders of magnitude smaller than an averaged 4-by-4 km satellite data pixel. Finally, as clouds covered the study area for most parts of the cruise (Table 2), the satellite data pixels were flagged as being affected by cloud reflectance. This can have a somewhat detrimental effect on the algorithms used in processing the satellite data, even though the pixels are still classified as valid. Note that all three caveats are challenges that any satellite remote sensing study faces, particularly in areas dominated by cloudy weather.

5.5. Measured vs. modeled light

For ArW and FMW, with very little impact of PIC, measured and modeled E_0(PAR) agreed quite well, as z_10 (n=6) of the two data sets were on average within 2.7 m of each other (Fig. 10). This verified that we could successfully model the effect of phytoplankton and CDOM on the underwater light field over a wide range of conditions; midday to midnight sun and fog to partly overcast. We thereby concluded that discrepancies between measured and modeled E_0 represented the optical effect of PIC on attenuation.

5.6. The impact on E_d of phytoplankton, CDOM and PIC along the transect

As described in Section 4.6, we could now quantify the impact of each of the optical components independently of the bb-based PIC calculations (Fig. 11). Phytoplankton and CDOM shifted the peak of E_d(PAR) from 470 to 530 nm for stations 238 and 232, and 550 nm for station 234. The presence of PIC shifted the peak further to 546 nm for stations 238 and 232, and 555 nm for 234. The effect of this “green shift” of the underwater irradiance is addressed in Section 5.7. PIC had a significant effect on both the shape and magnitude of the E_d spectra (Fig. 11). By taking the ratio of modeled E_d(PAR) without PIC and E_d(PAR) measured in the field (which includes PIC), the rate of spectral attenuation of light due to PIC can be calculated. These attenuation rates show remarkable similarity between stations, with the highest peak at 437–438 nm, and two other peaks on the red “tail” at 602 and 660–661 nm. Note that the 20 nm bandwidth of the model prevents concluding the exact wavelengths. However, the consistency corroborates that coccolith scattering, and thus the light attenuation observed in the present study, may take on different spectral shapes between coccolithophore blooms in different geographic areas, important for algorithm development for these blooms (Ackleson et al., 1994; Gordon et al., 2009; Voss et al., 1998).

The average (±S.D.) z_m at full AW stations (n=6) was 20±5 m in the field, while calculated without PIC it would be 31±8 m. Such a reduction in light availability is likely to have an impact on primary production, as z_m would be confined to the upper, nutrient-depleted layer. Balch et al. (1991) hypothesized that the resulting limitation of light could reduce consumption of nutrients by primary production below the coccolith-laden waters, allowing more nutrients to reach the surface layer where E. huxleyi normally resides.

The average contribution to light attenuation by the different optical components in the three water masses was estimated based on the E_d spectra with the best matches of model and field data at z_10 (as measured in the field) ‘clearest natural waters’ (Smith and Baker, 1981); that is, the model output with no optical constituents in the water, from here on termed ‘clear water’. Modeling showed that by the time light reached z_10, about 25% of the clear water E_d(PAR) was still available in AW, while in FMW and ArW the numbers were 36% and 39%, respectively (Table 5). Phytoplankton was the dominating attenuator in AW and ArW, while CDOM dominated in FMW. FMW and ArW showed similar properties for these results as well. PIC attenuation was only sufficiently high to be quantified in AW, as an underestimation of the light levels at z_10 in the model resulted in
negative attenuation by PIC in ArW and FMW; on average \(-5 \pm 9\%\). This serves as an indicator of the precision of spectral $E_d(\text{PAR})$ in the model. PIC and phytoplankton represented the most variable factors in absolute concentrations, as CDOM concentrations were fairly constant across the Polar Front (Fig. 4, also see Hancke et al., this issue).

5.7. PUR and potential primary production

We estimated PUR [in photons (mg Chl $a$)$^{-1}$ s$^{-1}$] to 0.57 in ArW, 0.54 in FMW and 0.43 in AW, meaning that in ArW, phytoplankton would be 34% more efficient at absorbing light than in AW given the same intensity of $E_d$ (Fig. 12). This demonstrates the importance of spectrally resolving light and phytoplankton absorption in ecological modeling of primary production (e.g. Alver et al., this issue). Relative $PP_{pot}$ in AW was 1.8 $\times$ that of ArW, and 2.3 $\times$ that of FMW. In comparison, average mg Chl $a$ m$^{-3}$ in AW was 1.5 $\times$ that of ArW, and 3 $\times$ that of FMW. However, Chl $a$ concentrations were 5–10 $\times$ higher at the surface of AW than ArW and FMW (Fig. 4). This means that the algae residing in the upper, well-lit part of the water column were crucial to securing higher $PP_{pot}$ in AW. When removing PIC in the radiative model for $E_d(\lambda)$ in AW, $PP_{pot}$ at the high-PIC stations 232, 234 and 238 increased by 20–40%. The spectral effect of coccoliths on $E_d(\lambda)$ was comparatively small, as removing PIC increased PUR by 8%. This could benefit *Emiliania huxleyi* by allowing it to shade the nutrient-rich layer below while retaining the PUR value, as this species has a relatively low nutrient requirement (Balch et al., 1991; Paasche, 2001).

6. Conclusions and outlook

We have successfully modeled and quantified the impact of phytoplankton, CDOM and coccolith PIC on irradiance and potential primary production in a situation that followed a coccolithophorid bloom bordering the Polar Front in the Barents Sea. PIC in the form of coccoliths had a dramatic effect on the optical properties of the water column and was clearly detectable from calculated irradiance reflectance spectra and the derived backscattering spectra. In AW, PIC was responsible for 18% of the attenuation of $E_d(\text{PAR})$ and reducing the depth of the euphotic zone by \(-30\%\). This impact quickly diminished already in the FMW when approaching the Arctic side of the Polar Front on Storbanken, where the effect of PIC was negligible. PUR calculations showed that phytoplankton in ArW absorbed light 34% more efficiently than in AW. Even so, higher phytoplankton biomass situated closer to the surface ensured that $PP_{pot}$ in AW was 1.8 $\times$ that of ArW with a subsurface Chl $a$ maximum. Removing the effect of PIC in the radiative model resulted in a relatively small increase in PUR of 8%. This is an important discovery, corroborating...
that *E. huxleyi* is potentially shading its competition from growing in deeper, nutrient-rich layers without deteriorating the “quality” of the irradiance spectrum. Not accounting for PIC in ecosystem modeling during *E. huxleyi* blooms in the Barents Sea could result in an overestimation of primary production in the order of 20–40%.

The linear relationship between PIC derived from the backscattering calculations and remotely sensed (MODIS) PIC showed a slope coefficient of 1.10 with $R^2 = 0.70$. This corroborates the backscattering calculation model, although further validation is still needed.

While satellites currently provide estimates of PIC over large areas, their application is particularly limited in their sub-surface vertical extent and thus their estimations on the local light attenuation. As Polar Regions, including the Barents Sea, are chronically under-sampled, new platforms and sampling approaches offer promise of filling in these temporal and spatial gaps (Dickey et al., 2008) and addressing the impacts of climate change on these systems (see Feely et al., 2009; Schofield et al., 2010). As such, spectral irradiance reflectance and diffuse attenuation as utilized in this study can already be measured with autonomous underwater vehicles (AUVs) and profiling buoys. This represents a novel and promising method of mapping IOPs and the impact of coccolith PIC abundance, especially when coupled with radiative transfer modeling.

Table 5
Water-type averaged attenuation of $E_d$(PAR) in the Barents Sea in the event of an *E. huxleyi* bloom, due to optical components phytoplankton, CDOM and PIC at the depth of $z_{10}$ as measured in the field. N is the number of full stations used for this calculation as only the best matching field and model estimated $E_d$(PAR) profiles were chosen. Available light is the field measured $E_d$(PAR) as a percentage of the model-estimated, clear water $E_d$(PAR) at the same depth. Attenuation columns give how much of the clear water $E_d$(PAR) had been attenuated by each optical component by the time irradiance reached $z_{10}$.

| Water (type) | n | Available Light ($E_d$) Mean (%) | S.D. | Phytoplankton Mean (%) | S.D. | Attenuation of $E_d$ CDOM Mean (%) | S.D. | PIC Mean (%) | S.D. |
|--------------|---|--------------------------------|
| ArW          | 2 | 39 ±1                          | 36 ±2 | 26 ±1                  | <1    | 1                                  |       | 1            |
| FMW          | 3 | 36 ±1                          | 29 ±6 | 35 ±7                  | <1    | 11                                 |       | 7            |
| AW           | 3 | 25 ±2                          | 40 ±4 | 17 ±5                  | 5     | 18                                 | 7     | 7            |

Fig. 11. A–C: Relative effect on $E_d(\lambda)$ by optical constituents phytoplankton, CDOM and PIC at the 3 stations of highest $PI_{234}$. Full, black line is the measured available $E_d(\lambda)$ at $z_{10}$ normalized to 1 at the peak. All data are scaled relative to this. Dashed lines are model estimated $E_d(\lambda)$ at $z_{10}$, given for clear water (blue line), only Chl $a$ (green line) and Chl $a$ + CDOM (yellow line). The “PIC” area thus represents the light attenuated due to PIC present in the water. D: Attenuation calculated from the spectra in A–C. Full lines show the spectral ratio of attenuation due to PIC, that is Chl $a$ + CDOM estimated $E_d(\lambda)$ : measured $E_d(\lambda)$, while punctured lines represent the “PIC” area for stations 232 (green), 234 (violet) and 238 (orange). Color version is available online.

Fig. 12. Photosynthetically Usable Radiation (PUR) for phytoplankton in the Barents Sea at the midpoint of the euphotic zone ($z_{10}$) in Arctic (blue area) and Atlantic (red area) Water. PUR is the product of relative spectral downwelling irradiance [$E_d(\lambda)$, where $E_d$/(PAR) = 1] in ArW (blue line) and AW (red line) multiplied by the Chlorophyll a-specific absorption coefficient for phytoplankton at station 234 [$a_p(\lambda)$, orange line] (Morel, 1978). Note that $E_d(\lambda)$ for FMW (green line) at $z_{10}$ is almost identical to that of ArW. Color version and source data are available online.
Acknowledgments

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Appendix A: Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.jmarsys.2012.07.002.

References


