COCCOLITHOPHORES

Optical properties, ecology, and biogeochemistry

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Griet Neukermans PhD in optical oceanography MSc. Mathematics (VUB-Belgium) MSc. Oceans & Lakes (VUB-Belgium)

Core expertise : development and application of remote and in situ optical sensing of marine particles



Remote sensing and light scattering properties of suspended particles in European coastal waters

(PhD, ULCO-France, advisors: H. Loisel and K. Ruddick)



Optical detection of particle concentration, size, and composition in the Arctic Ocean (Postdoc SIO UCSD-USA, advisors: D. Stramski and R. Reynolds)



Impact of climate change on phytoplankton blooms on the Arctic Ocean's inflow shelves









Remote sensing of ocean colour and physical environment + Modeling the light scattering properties of coccolithophores (with G. Fournier)

(Banting Postdoctoral Fellow, ULaval-Canada, advisor: M. Babin)

Poleward expansion of coccolithophore blooms and their role in sinking carbon in the Subarctic Ocean

(Marie Curie Postdoctoral Fellow, LOV-France, advisor: H. Claustre + co-advisors: G. Beaugrand and U. Riebesell)

Optical remote sensing + Ecological niche modeling + optical modeling + Biogeochemical-Argo floats



















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- Coccolithophore biology and ecology
 - Diversity, distribution, and biomass
- Remote sensing of coccolithophores and their calcite mass (PIC)
 - Bloom observations and classification
 - Quantifying PIC in the ocean
 - Caveats of remotely sensed PIC
- Optical properties of coccolithophores
 - Scattering, backscattering, and absorption
 - Reflectance
 - Birefrigence
- Some applications of optical oceanography in coccolithophore research
 - Ecology (environmental control of coccolithophore blooms, phenology, ocean albedo)
 - Climate change impacts
 - Biogeochemistry (influence on pCO₂, calcite ballast effect)

What are coccolithophores?



- Calcifying phytoplankton
- Haptophyta; Prymnesiophyceae
- Produce CaCO₃ scales (coccoliths)
- About 200 species
- Occur throughout the world ocean
- 5 μm ≤ D ≤ 40 μm
- Considered as a single functional group within the phytoplankton (>biogeochemistry)
- Comprise about 10% of global phytoplankton biomass
- Major CaCO₃ producers in the open ocean (besides forams and pteropods)

Coccolith production



Coccolithus pelagicus D = 10-40 μm

$$Ca^{2+} + 2 HCO_3^- \rightarrow CaCO_3 + CO_2 + H_2O$$

Produces about 1 coccolith every 1.5-2h



Video microscopy Courtesy: Alison Taylor

Taylor et al. 2007 Eur. J. Phycol.

Coccolith function

Why do coccolithophores calcify?



Coccolithophore distribution and diversity

Coccolithophore species exhibit distinct vertical and latitudinal zonation.



- Temperature and light are key drivers of latitudinal diversity patterns
- Diversity is highest in the lower latitudes
- Diversity is lowest at higher latitudes, where assemblages are often dominated by the bloom-forming species *E. huxleyi* (*Ehux*)

Coccolithophore distribution and diversity

Coccolithophore species exhibit distinct **vertical** and latitudinal **zonation** Throughout the euphotic and aphotic zone, according to their ecological preferences.

Monteiro et al. (2016 - Sci. Adv.)



Coccolithophore biomass distribution

- Most comprehensive in situ dataset of coccolithophore biomass from microscopy or flow cytometry (1929-2008)
- About 11000 observations of total coccolithophore abundance and biomass (O'Brien et al., 2013 ESSD)



Coccolithophore PIC in the ocean

- OCRS provides daily global observations of PIC
- ...but the algorithm has limitations...





Remote sensing of coccolithophores and their calcite mass (PIC): a chronological overview of approaches

- 1. Holligan et al. (1983): bloom observations from CZCS Rrs at 550nm
- 2. Balch et al. (1991): bloom observations from AVHRR + in situ IOPs
- 3. Brown and Yoder (1994): coccolithophore bloom classifier for CZCS
- 4. Gordon et al. (2001): quantification of PIC (high), NASA's standard algorithm
- 5. Balch et al. (2005): quantification of PIC (low-med), NASA's standard algorithm
- 6. Shutler et al. (2010): coccolithophore bloom extent in shelf seas and coastal zones probably the only case 2 algorithm
- 7. Sadeghi et al. (2012): SCIAMACHY, based on absorption
- 8. Moore et al. (2012): bloom classifier based on fuzzy logic for all OC sensors
- 9. Mitchel et al. (2017): quantification of PIC based on reflectance-difference approach

First observations of coccolithophore blooms

MODIS natural-color image

August 2011

LANDSAT MSS4 (0.5-0.6µm)

© NASA

- From ships in Norwegian fjords:

 unusual milky turquoise colour caused by
 enourmous concentrations of the calcareous
 flagellate *Coccolithus huxleyi* up to 115 x 10⁶ cells/L
 in surface water» (Birkenes and Braarud 1952; Berge, 1962).
- First blooms discovered from space:
 - Landsat in 1977 (Le Fevre et al., 1983)
 - CZCS in 1982 + ship (Holligan et al. 1983)







First OCRS observations of blooms - CZCS

Ship- and satellite-borne observations of *Ehux* blooms at a European continental shelf edge.





Significant positive correlation was found between reflectance from each of the CZCS channels (443, 520, and 550 nm) and the surface abundance of coccolithophores.

Bloom observations from AVHRR (1)

Ship- and satellite-borne observations of Ehux blooms in the Gulf of Maine



Balch et al. (1991) and Ackleson and Holligan (1989) suggested that the high backscattering was caused principally by the presence of **detached coccoliths**, rather than by coated cells.

"Free coccoliths do the bulk of the light scattering in *Ehux* blooms but reflectance is more likely a function of coccoliths and (coated) cells." [Balch et al. (1991)]

Bloom observations from AVHRR (2)

First study connecting in situ biogeochemical and optical measurements with satellite data (AVHRR) during an *Ehux* bloom South of Iceland in 1991



Bloom area: 0.5 million km² (size of Spain)

Levels of dimethylsulphide (**DMS**) in surface waters were high compared to average ocean values, with the greatest concentrations in localized areas

Characterized by high rates of Photosynthesis, calcification, and grazing by microzooplankton.

Coccolith production had a significant impact on the state of the in-water **pCO₂**

Fig. 3. AVHRR visible (channel 1) images of the central area of the *E. huxleyi* bloom to the south of Iceland for (a) Jun 15; (b) June17; (c) June 19; and (d) June 21, 1991, showing changes in the distribution of coccolith reflectance due to water motion. The images were all received on the early afternoon passes of NOAA 11. The speckled appearance of the SW quadrant of Figure 3d is due to atmospheric effects.

Coccolithophore blooms

Two known bloom forming species ("bloom" means >10⁶ cells / L)



Coccospheres, D 5 to 10 μ m; coccoliths, 2 to 5 μ m long.

Ubiquitous species, dominant bloom-former in temperate and subpolar waters.



Coccospheres, D 6 to 10 μm; coccoliths, 3.5 to 6 μm long.

Predominantly low-latitude warm-water eutrophic species. More widespread in the Pacific than in the Atlantic Ocean.

Ehux is thought to be **unique** in overproducing coccoliths and then shedding the excess ones into the water (Paasche 2002) -> hardly any of the open-ocean bright waters are attributable to species other than *Ehux*. But see (Blackburn and Cresswell, 1993) for *G. oceanica* bloom in AUS.

Young, J.R., Bown P.R., Lees J.A. (2017) Nannotax3 website. International Nannoplankton Association. www.mikrotax.org/Nannotax3

Emiliania huxleyi (Ehux)

Emiliania huxleyi Home Page Welcome to the home page for "Ehux"

http://www.noc.soton.ac.uk/soes/staff/tt/eh/

Created by Toby Tyrrell at Southampton University

A model system approach to biological climate forcing. The example of *Emiliania huxleyi*

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ABSTRACT

Westbrock, P., Brown, C.W., Van Bleijswijk, J., Brownlee, C., Brummer, G.J., Conte, M., Egge, J., Fernández, E., Jordan, R., Knappertsbusch, M., Stefels, J., Veldhuis, M., Van der Wal, P. and Young, J., 1993. A model system approach to biological climate forcing. The example of *Emiliania huxleyi*. Global Planet. Change, 8: 27-46.

Particulate inorganic carbon (calcium carbonate mineral) is produced by pelagic calcifying organisms in the upper layers of the open ocean, it sinks to the deep sea, is partly dissolved and partly stored in the geological archive. This phenomenon, known as the carbonate pump, is an important component of the global carbon cycle and exerts a major influence on climate. The amount of carbonate mineral produced depends on the evolutionary and ecological success of calcifying pelagic organisms. The formulation of adequate predictive carbonate pump modules raises the problem that the behaviour of this highly diverse set of organisms needs to be taken into account. To overcome this difficulty, we propose a "model system" approach, whereby a single representative organism, the coccolithophore *Emiliania huxleyi*, is investigated in detailed interactive experimental and modelling studies. To construct a comprehensive model of the carbonate pump, subsequent research is envisaged on additional representative organisms, but this work is likely to be facilitated by the experience gained with *E. huxleyi*. The model system approach permits (1) an emphasis on the non-linear character of the fluxes; (2) a focus on the coupling of the carbonate pump with other climatically important phenomena—the organic carbon pump and DMS production; and (3) exploitation of the experimental accessibility of the *E. huxleyi* system.

Coccolithophore bloom classification - CZCS

Brown and Yoder (1994)



Supervised multispectral classification scheme from weekly CZCS data (1978-1986) from nL_w magnitude and band-ratios.

Coccolithophorid blooms annual coverage: 1.4 x 10⁶ km²



Misclassifications of blooms due to similarity with Whitings Sediments

Coccolithophore bloom classification

Moore *et al.* (2012), RSE

Generalized bloom classifier for all ocean colour sensors (SeaWiFS, MODIS, MERIS) based on fuzzy logic.

Detection levels: 1500-1800 cells/mL and 43000-78000 liths/mL



Global annual coccolithophore bloom coverage of about 2.75 x 10^6 km²: 2 x 10^6 km² in Southern Hemisphere and 0.75 x 10^6 km² in Northern Hemisphere.



Figure 1. $b_b(546)$ in m⁻¹ retrieved from the July 30, 1999 SeaWIFS image of Plymouth, UK. Areas of enhanced backscat-

PIC in blooms from SeaWiFS

Gordon *et al*. (2001)

Heart of the algorithm:

 $b_{bpic}(546 \text{ nm}) = 1.6x[PIC \text{ in mol m}^{-3}]-0.0036$ $b_{bpic}(\lambda) = b_{bpic}(546)x(546/\lambda)^{1.35}$ [Based on in situ measurements by Balch *et al.* (1991)]

3-band algorithm retrieving ρ_w (546 nm) from SeaWiFS reflectance in Red and NIR bands (670, 765, 865nm)

Suitable for high concentrations of CaCO₃, when B-G bands often saturate (not accurate for PIC concentrations < 3 mmol m⁻³)

Assumptions:

- ρ_w(765, 865nm)=0
 - $ho_w(\lambda)=b_b(\lambda)/(6(a_w(\lambda)+b_b(\lambda)))$ with $\lambda=670$ nm

maximum RMS error of the algorithm is +/- 15 μ g/L (or 1.2 mmol m⁻³) = about 5-10% of PIC in dense bloom (Balch, 2004)

PIC from MODIS

Balch et al. (2005)

Heart of the algorithm (same as Gordon algo): $b_{bpic}(546 \text{ nm}) = 1.6x[PIC \text{ in mol m}^{-3}] - 0.0036$ $b_{bpic}(\lambda) = b_{bpic}(546)x(546/\lambda)^{1.35}$

PIC is retrieved from a LUT based on semianalytical OCRS model of Gordon *et al.* (1988)

Validated with in situ data of b_{bpic} , PIC, Chla, and L_w mainly in Maine waters (*Ehux* dominated)

Retrieval uncertainty: due to natural variability in phytoplankton-detritus b_b corresponds to 25 x 10⁶ coccoliths/L = 5 µg PIC/L = 0.41 mmol PIC/ m³

Major limitations:

- dependency on the reflectance model (assumed constant phyto-detritus b_b)
- absolute radiance -> sensitivity to atmospheric correction errors
- Estimate of "excess backscatter" -> particles other than PIC may also cause excess backscatter



NASA's standard PIC algorithm

"Balch and Gordon"



a **hybrid** of 2-band approach of Balch *et al.* (2005) and the 3-band approach of Gordon *et al.* (2001)

The 2-band approach of Balch et al. (2005) is applied, unless reflectance values fall outside the bounds of the LUT (<40 μ g PIC/L or 3 mmol PIC/m³); then the 3-band algorithm of Gordon et al. (2001) is used.

The algorithm is applicable to all current ocean color sensors.

Mainly validated in Maine and Southern Ocean waters.

PIC algorithm caveats

False positives for high PIC (highly reflective waters) produced by:

• Whitings = patches of suspended fine-grained calcium carbonate



https://earthobservatory.nasa.gov/

(Dierssen et al., 2009 – Biogeosciences)



- High concentrations of empty diatom frustules (e.g. on shallow shelves, Broerse et al., 2003) or suspended sediments
- In polar waters: Floating sea-ice
- Bubbles
- Phaeocystis foam

Alternative PIC algorithm

Reflectance difference approach, inspired by Hu et al. (2012) for Chla

Mitchell et al. (2017)



More resistant to atmospheric correction errors and residual errors in sun glint corrections than the Balch *et al.* (2005) algorithm.

Potential to replace the Balch et al. (2005) algorithm currently being investigated

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Light absorption properties of coccoliths

Measurements of $a_{\rho}(\lambda)$ (filter-pad technique) in *Ehux* bloom in the Gulf of Maine.



Light absorption by coccoliths is negligible

Consistent with the absorption properties of calcite for which the absorption is negligible even in the far UV (Palik, 1998- *Handbook of Optical Constants of Solids*).

Fig. 9. Particulate absorption spectrum (m^{-1}) from station 8 at 5 m. Data represent two scans, one of a glass-fiber filter through which raw coccolithophore bloom water was passed (curve n) and an identical filter through which bloom water was passed following dissolution of coccoliths (curve a).

Light absorption by Ehux cells

Measurements from Ehux cultures



Typical Chla content for Ehux = 0.24 pg Chla/cell (Ahn et al., 1992 – Deep Sea Res.), up to 0.4 pg Chla / cell (Daniels et al., 2014 – Biogeosciences)

-> 0.24 pg - 0.40 pg Chla x 10⁶ cells/L in a bloom = 0.24-0.40 μ g/L in a bloom.

Light scattering properties

They are made of calcite with refractive index = 1.20 relative to water (other refractive indices for reference: 1.05 for POC, 1.07 for BSi), which makes them highly efficient light scatterers



Figure 3. Spectral variations of Q_b within the 400-750 nm range of various phototrophic and heterotrophic organisms as experimentally determined (Morel and Ahn, 1990, 1991).

Light scattering properties of calcite particles in the ocean



Light backscattering vs. PIC



Neukermans and Fournier (2018) – F.Mar.Sci.

basis of NASA's standard PIC algorithm: b_{bpic}/PIC = constant

Optical modeling studies (ADA, DDA) show that b_{bpic} /PIC does not depend much on whether coccoliths are attached to are freed from the coccoshpere

(see also Gordon et al., 2009, Appl. Opt.)

Light backscattering properties of *Ehux*

Strongly depend on coccolith morphology (and size, indirectly)



Model of E. huxleyi coccolith

(Fournier and Neukermans, 2017, Opt. Expr.; Neukermans and Fournier, 2018, F.Mar.Sci.)

Light backscattering properties of *Ehux*



Fig. 6. Specific b_b coefficients (b_b^*) as a function of wavelength for both the BP-derived and GASM-derived measurements. Open symbols are the GASM-derived coefficients; filled symbols are the BP-derived coefficients. Triangles correspond to coccoliths, diamonds to plated cells, and circles to naked cells. Also shown is the power law fit to each component (as discussed in the text). The exponent found for each component was -1.4, -1.2 and -1.0 for coccoliths, plated cells, and naked cells, respectively.

Ehux has various morphotypes



TABLE 1. Classification of morphotypes of Emiliania huxleyi.

Morphotype in this study	Morphology of distal shield	Morphology of central area	Length of distal shield	Comparable morphotypes in literature
Туре А	Moderate-heavily calcified elements	Grill	<4 µm	Warm type (McIntyre and Bé 1967)
Type B	Lightly calcified elements	Solid plate	≥4 μm	Type B (Young et al. 2003)
Type B/C	Lightly calcified elements	Solid plate	<4 µm	Type B/C (Young et al. 2003)
Type C	Lightly calcified elements	Solid plate	<3.5 μm	Cold type (McIntyre and Bé 1967) Type C (Young et al. 2003)
Туре О	Lightly calcified elements	Open	Varied in size	Subarctic type (Okada and Honjo 1973)
				Type B (Hagino et al. 2005)
Type R	Reticulofenestra-like heavily calcified distal shield elements	Grill	<4 µm	Type R (Young et al. 2003)
var. corona	Moderately calcified elements with elevated central tube	Grill	3.5–4.5 μm	var. <i>corona</i> (Okada and McIntyre 1977)

Hagino et al., 2011 (J. Phycol)

Different *Ehux* morphotypes are expected (in theory) to have different magnitude and spectral shapes for backscattering



Images: Young, J.R., Bown P.R., Lees J.A. (2017) Nannotax3 website. International Nannoplankton Association. www.mikrotax.org/Nannotax3

The milky-turquoise hue of *Ehux* bloom waters?

700

Ehux bloom in the Barents Sea, 17 August 2011.



True Colour Composite from MODIS Aqua

The milky-turquoise hue of *Ehux* bloom waters?



Neukermans and Fournier, F.Mar.Sci. (2018)

Calcite is strongly birefrigent



"Birefringence refers to the ability of a mineral crystal to split an incident beam of linearly polarized light into two beams of unequal velocities (corresponding to two different refractive indices of the crystal), which subsequently recombine to form a beam of light that is no longer linearly polarized."

Birefringence can be detected by measuring the changes in the polarization of light passing through the material (e.g., polarized light microscopy)

Guay and Bishop, *Deep Sea Res.* (2002)

https://en.wikipedia.org/wiki/Birefringence

parallel polarizers

s crossed (90°) polarizers



Provided the basis for an in situ marine PIC sensor (the Carbon Flux Explorer – Bishop *et al.*, 2016, Biogeosciences)

Spectrophotometer technique= transmittance + linear polarizers

Carbon Flux Explorer

Designed to perform sustained high-frequency observations of POC and PIC sedimentation within the ocean's twilight zone



Baffle Funnel Down light w. polarizer Settling Column Dark field light Cleaning Sample stage Polarizer Rotator Imager CPU microcontroller Tensionina rod for bottom cap **Batteries**

marine-snow aggregate of about 1cm



Image resolution is 13 μm.

Bright spheres = 200 μm sized foraminifera shells

Not (yet) fully autonomous (due to image processing)

Resolution too coarse to resolve coccolithophores...

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Environmental control of coccolithophore blooms



Large-scale seasonal blooms of *Ehux* detected by OC satellites are generally associated with:

- Temperate and subpolar waters
- After a diatom Spring bloom (succession)
- Relatively high critical irradiances
- Stable water column
- Declining nutrients





[see Iglesias-Rodrigez et al., 2002; Tyrrell and Mercio, 2004; Balch 2004; Signorini and McClain, 2009]

Succession or coexistence of phytoplankton populations Margalef's (1978)

Barber and Hiscock (2006)



Succession: shelf regions, upwelling areas, and the HLNA in support of Margalef's suggestion that environmental changes promote the proliferation of one taxa at the expense of another.

Coexistence: across much of the open ocean in support of Barber and Hiscock (2006)'s suggestion of coexistence through differences in biomass accumulation rates, while actual competition between the two populations is kept in check through variability in nutrient uptake rates and shifts in the dominant grazers and the overall food web structure.

Coccolithophore phenology

Seasonal variability in PIC is identified across much of the global ocean



Based on MODIS 8-day PIC climatology (2003-2012)

Ehux blooms: brighter surface ocean, darker deeper down



Ehux blooms increases ocean albedo

Contribution to global annually averaged planetary albedo is about 0.13%

(Tyrrell et al., 1999 - JGR)

Figure 2. Photon budgets for water with (A) no particulate inorganic carbon (PIC) vs. (B) 300 µgPIC L⁻¹, Values are based on incoming irradiance of 1100 µEin m⁻² s⁻¹, wind speed = 5 m s⁻¹, cloud cover = 25%, chi = 0.75 µg L⁻¹, and solar zenith angle = 45°. T Einstein = 1 mole of photons (or Avogadro's number of photons: 6.02 x 10²³). Optical modeling results redrawn from Tyrell et al. (1999)



But, strong local effects:

Ehux blooms shoal the euphotic zone, diminishing the light available for deeper algal species,

limiting photosynthesis at depth by 20–40% where nutrient levels are otherwise sufficient

(Hovland et al., 2013- J. Mar. Sys.)

Poleward expansion of *Ehux*

Proposed by Winter *et al.* (2014 – *J. Plankton Res.*), based on OCRS (CZCS and SeaWiFS) and in situ data.



Coccolithophore data within 30°-70°S /130°-170°E

Poleward expansion of *E. huxleyi* blooms: On an Arctic inflow shelf (Barents Sea)

Neukermans et al. (Glob. Change Biol., 2018)



Approach:

Combine long-term (1980s-2016) remote sensing data of *Ehux* blooms with remote sensing data of the physical environment (sea surface temperature and sea ice)



Poleward expansion of *E. huxleyi* blooms



Global mean rate for: marine species = 7.2 km/yr, phytoplankton = 35.8 km/yr, zooplankton = 14.2 km/yr

Neukermans *et al.* (*Glob. Ch. Biol., 2018*)

Poleward expansion of *E. huxleyi* blooms



Poleward expansion in the Barents Sea is driven by increased intrusion and warming of Atlantic waters

Role of Coccolithophores in Ocean carbon cycle



Carbonate counter pump: $CaCO_3$ production and its transport to depth, releases CO_2 in the surface layer.

The relative strengths of these two pumps (rain ratio) largely determine the biologically mediated ocean atmosphere CO_2 exchange.

Rost and Riebesell (2004)

Role of Coccolithophores in Ocean carbon cycle

 $Ca^{2+} + 2 \ HCO_3^- \rightarrow CaCO_3 + CO_2 + H_2O$

Using 10 years of SeaWiFS data of classified *Ehux* blooms in the North Atlantic and climatologies of pCO₂ in air, seawater, salinity, solubility and gas transfer velocity :

It was estimated that *Ehux* blooms can **reduce the annual net sink of atmospheric CO₂ by 3– 28 %.**



Fig. 4. Spatial distribution of the maximum impact of Emiliania huxleyi on the monthly air-sea CO₂ flux for years 1998-2007. (a) Percentage increase in seawater partial pressure $pCO_2(0-35\%)$; (b) Percentage decrease in air-water partial pressure difference ΔpCO_2 (0-231%); (c) Percentage decrease in air-sea CO₂ flux (0-155%).

Shutler et al. (2013–Biogeosciences)

Role of Coccolithophores in Ocean carbon cycle

Ballast hypothesis: *E. huxleyi* calcite material ballasts organic carbon by increasing sinking speed and protecting organic carbon from remineralisation (François et al., 2002)

widely debated and poorly understood

Hampered by paucity and limited resolution of traditional particle flux measurements (from sediment traps and radiochemical tracers)





Can we examine calcite ballasting using bio-optical measurements on Biogeochemical-Argo floats?

- 1. Can we identify coccolithophore blooms from floats?
- 2. Can we quantify associated sinking particle (carbon) fluxes?



Neukermans et al. (in prep.)



Neukermans et al. (in prep.)





have a c_p sensor and sampled a coccolithophore bloom



have a c_p sensor and sampled a coccolithophore bloom

