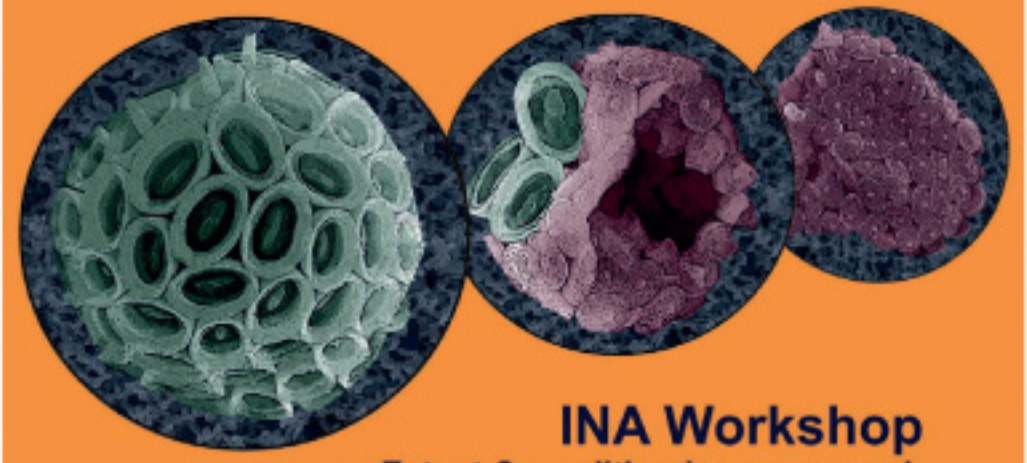
Journal of Nannoplankton Research

volume 34 | special issue | october 2014

COCCOLITHOPHORES 2014



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A mixed life-cycle stage bloom of *Syracosphaera bannockii* (Borsetti and Cati, 1976) Cros et al. 2000 (Bay of Biscay, April 2010)

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Abstract: High concentrations (464 cells ml-1) of *Syracosphaera bannockii* have been identified for the first time, in the Bay of Biscay during April 2010. These high concentrations combined with coccolithophore community dominance (~87%) indicated that a bloom of *S. bannockii* had formed. While the bloom consisted mostly of heterococcolith coccospheres, both holococcolith coccospheres and holococcolith-heterococcolith combination coccospheres were observed. This is only the second time that combination coccospheres of *S. bannockii* have been observed.

Keywords: *Syracosphaera bannockii*, coccolithophore bloom, combination coccospheres,

1. Introduction

Syracosphaera is a large and diverse genus of coccolithophores, and forms a significant proportion of the extant coccolithophore community (Young et al., 2003). Despite this, *Syracosphaera* coccolithophores are poorly understood, with only one species, *Syracosphaera pulchra*, maintained and studied in culture (Geisen et al., 2002; Young et al., 2003; Fiorini et al., 2011). Moreover, *S. pulchra* may not be a typical species of this genus since it is significantly larger (~15μm) and appears more heavily calcified than most *Syracosphaera* species.

As part of a multi-year survey of coccolithophores in the Bay of Biscay (Daniels et al., 2012; Smith et al., 2012), high concentrations of *Syracosphaera bannockii* (Borsetti and Cati, 1976) Cros et al. 2000 were observed on one transect in April 2010 (Daniels et al., 2012). *Syracosphaera bannockii* is a coccolithophore with multiple life-cycle stages: a heterococcolith bearing haploid phase, and a holococcolith bearing diploid phase (Cros et al., 2000; Geisen et al., 2002; Young et al., 2003). It has only been relatively recently described by Cros et al. (2000), from combination coccospheres of the holococcolith *Zygosphaera bannockii* and a previously undescribed *Syracosphaera* heterococcolith. This combination was described as *S. bannockii*, since the genus *Syracosphaera* has priority over *Zygosphaera* (Geisen et al., 2002). While this was the first description of *S. bannockii* heterococcoliths, they are very similar to *Syracosphaera orbiculus* and *Syracosphaera delicata*, and may represent intraspecific variation (Young et al., 2003). Little is known about the biogeographical distribution of *S. bannockii*, but it has been reported in communities in both the North and South Atlantic (Balestra et al., 2004; Boeckel and Baumann, 2008; Poulton et al., 2010; Charalampopoulou et al., 2011). Here we present the first evidence that *S. bannockii* can form relatively high cell densities (>400 cells ml^{-1}), in this case consisting of both the heterococcolith and the holococcolith life-cycle phases.

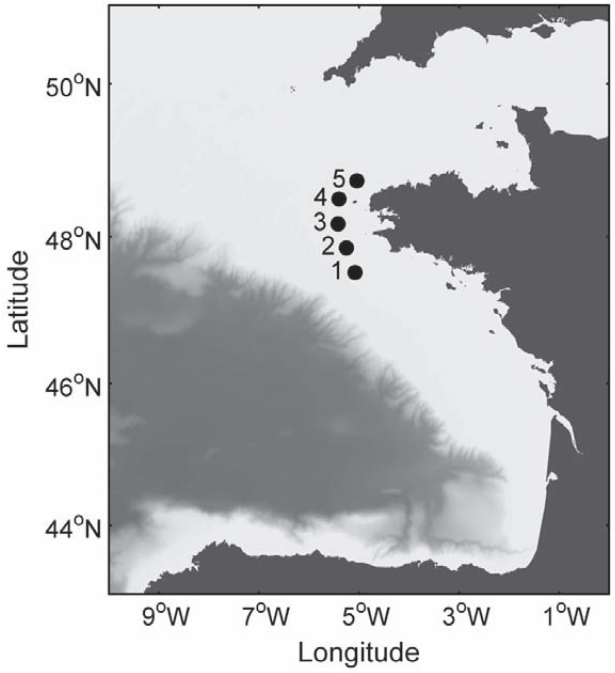


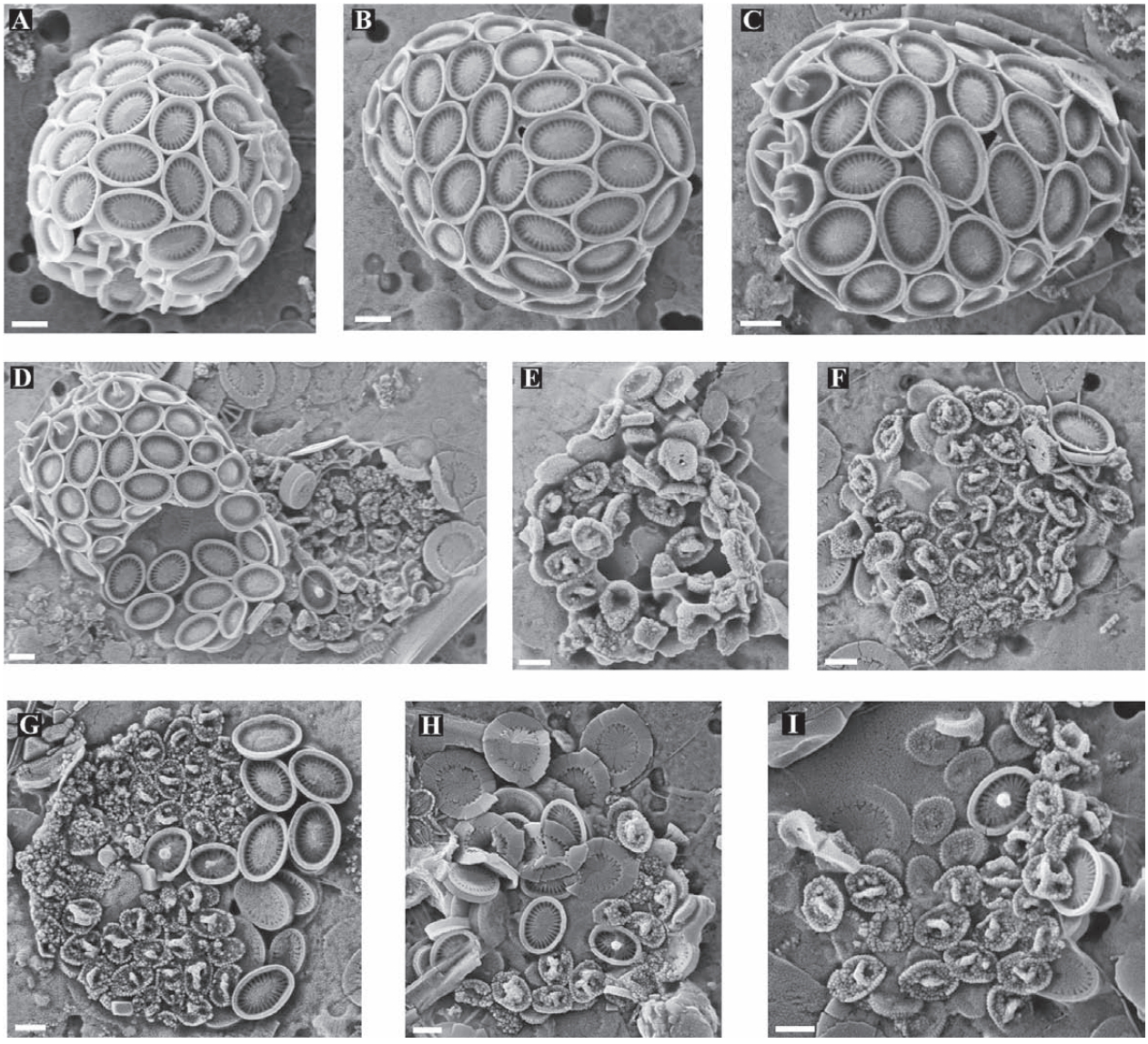
Figure 1. Map of the Bay of Biscay showing the location and station numbers of the 5 stations at which *Syracosphaera bannockii* was found.

2. Material and methods

Samples were collected aboard the MS *Pride of Bilbao* from the Bay of Biscay between 2006 and 2010, with the samples described here collected on the 15th April 2010. Water samples were collected from the ship's seawater intake supply (5m depth) and filtered on to 0.8 μm polycarbonate filters. Samples were collected every 4 hours, corresponding to an approximate resolution of 40 km. Further cruise and sampling details are documented in Daniels et al. (2012). The samples were imaged on a Leo 1450VP scanning electron microscope (SEM). Specimens were initially observed on low resolution automatically captured images, to confirm the identification of *S.*

Plate 1

Syracosphaera bannockii. A–C. Heterococcolith coccospheres with both body coccoliths and circum-flagellar coccoliths with spines. D. Heterococcolith coccosphere with a holococcolith coccosphere next to it. E–F. Holococcolith coccospheres. G–I: Combination coccospheres of both heterococcoliths and holococcoliths, surrounded by exothecal coccoliths. All scale bars are 1µm.



bannockii the sample with the most abundant material was reimaged with manual focussing and image capture. Coccolithophore species were determined following (Young et al., 2003), with cells counted from 225 fields of view (Daniels et al., 2012).

3. A bloom of Syracosphaera bannockii

Analysis of the samples collected in April 2010 identified *S. bannockii* in 5 consecutive samples (Table 1), collected from the Ushant shelf region of the Bay of Biscay (Figure 1), in waters with sea surface temperatures ranging from 10.8–11.1 °C and sea surface salinity 35.0–35.2. Other coccolithophore species observed in relatively low abundances (<37 cells ml^{-1}) in these samples included: *Acanthoica quattrospina*, *Algirosphaera robusta*, *Calciopappus caudatus*, *Coccolithus braarudii* HOL, *Coronosphaera mediterranea*, *Emiliania huxleyi, Pappomonas* sp., *Syracosphaera anthos*, *Syracosphaera molischii*, *Syracosphaera ossa* and *Syracosphaera* sp.

The identification as *S. bannockii* type coccoliths is indicated by the combination of simple murolith body coccoliths and irregular-planolith exothecal coccoliths. Three species are included in this grouping by Young et al. (2003) - *S. bannockii, S. orbiculus* and *S. delicatus*, although it has been suggested that *S. delicatus* is a junior synonym of *S. orbiculus* (Young et al. 2014, Nannotax). The specimens imaged at high resolution (Plate 1) show

Station	Latitude (°N)	Longitude (°W)	S. bannockii (cells ml^{-1})	Life-cycle stage contribution (%)		
				HET	HOL	combination
1	47.52	5.08	8	93	0	7
2	47.85	5.25	464	92	4	4
3	48.17	5.42	369	97	2	1
4	48.50	5.40	88	99	1	0
5	48.74	5.04	16	100	0	0

Table 1. Station locations and the abundance of *Syracosphaera bannockii*, with the percentage contribution from coccospheres of different life-cycle stages. HET – heterococcolith coccospheres. HOL – holococcolith coccospheres. combination – holococcolith-heterococcolith combination coccospheres.

broad rims on the body coccoliths and the exothecal coccoliths do not have ridges, these characteristics indicate that they are *S. bannockii*. There was no evidence from lower resolution images that there was any significant morphological variation within the species. The associated holococcoliths show variable development of a central opening but this variation was previously noted within *S. bannockii* holococcoliths (Cros et al. 2000, Young et al. 2003).

Although *S. bannockii* has been observed in different areas of the North Atlantic (Balestra et al., 2004; Poulton et al., 2010; Charalampopoulou et al., 2011), it has never been reported to dominate the coccolithophore assemblage. Here we observed that in samples 2–4 (Table 1), *S. bannockii* dominated the coccolithophore community with particularly high abundances in samples 2 (464 cells ml^{-1}) and 3 (369 cells ml^{-1}). While these abundances are below the arbitrary 1000 cells ml^{-1} threshold sometimes used to define an *E. huxleyi* bloom (Tyrrell and Merico, 2004), the significant abundances combined with the fact that *S. bannockii* formed ~87% of the total coccolithophore assemblage, suggests that this can be defined as a bloom of *S. bannockii*. Very few coccolithophorids other than *E. huxleyi* have been reported to form blooms; *C. pelagicus* (Milliman, 1980; Tarran et al., 2001) and *Gephyrocapsa oceanica* (Blackburn and Cresswell, 1993) have both been observed in high concentrations (>1000 cells ml^{-1}), while a coccolithophore bloom in southern Benguela waters was attributed to *Syracosphaera pulchra* (Weeks et al., 2003). Therefore we believe that this is the first report of a bloom of *S. bannockii* or any small species of *Syracosphaera*.

Emiliania huxleyi blooms have been observed across multiple years in the Bay of Biscay (Harlay et al., 2010; Harlay et al., 2011; Daniels et al., 2012). However, these blooms occur later in the season (May – June) than this *S. bannockii* bloom, with the 2010 *E. huxleyi* bloom observed in May (Daniels et al., 2012). For high net growth rates associated with bloom formation, conditions must be favourable for high gross growth rates of *S. bannockii*, while mortality through viral lysis or grazing must be low. Factors associated with high *E. huxleyi* abundance include high irradiance, shallow mixed layers, high temperatures and low grazing pressure (Tyrrell and Merico, 2004; Raitsos et al., 2006). However, whilst *S. bannockii* remains absent in culture collections, it is difficult to examine the physiology of this species or the environmental factors which favour faster growth of this species relative to other more renowned bloom forming species (e.g. *E. huxleyi*).

Estimating the areal extent of this bloom from a single transect requires the assumption of a circular distribution and interpolation between samples. With the highest concentrations measured ~40km apart, and lower but significant concentrations spanning a further ~120km, this suggests that the central bloom covered ~1250 km^2, with lower abundances in the surrounding ~18000km^2. While these estimates carry a significant uncertainty, they suggest a bloom of significant magnitude.

The biogeochemical impact of this bloom cannot be easily assessed as we know so little about *S. bannockii*, however using measurements of heterococcolith cellular geometry from SEM images, we can estimate cellular calcite (Young and Ziveri, 2000). Cells of *S. bannockii* had on average, 45 – 46 coccoliths per cell, with an average coccolith length of 2.2 μm. Using a "small *Syracosphaera*" shape factor from Young and Ziveri (2000), we estimate a cellular calcite value of 0.19 pmol C cell^{-1}, which is around half of that found in a (nutrient replete) *E. huxleyi* cell (0.39 – 0.49 pmol C cell^{-1}, Poulton et al., 2010; Daniels et al., 2014). This is a significantly smaller source of calcite, particularly as higher abundances of *E. huxleyi* have been observed in the Bay of Biscay (1000 – 8000 cells mL^{-1}, Harlay et al., 2010; Daniels et al., 2012). However, in terms of its contribution towards standing stocks of organic carbon and chlorophyll *a*, *S. bannockii* is ~8 times larger (~400 μm^3) in terms of cell volume (and hence cellular carbon/chlorophyll content, see Daniels et al., 2014) than *E. huxleyi* (50 μm^3), and on a species-specific level is therefore a potentially more important contributor to primary production and the biological carbon pump.

4. Life-cycle stages of Syracosphaera bannockii

The bloom of *S. bannockii* was comprised of both life-cycle stages. The majority (92 – 100 %) of coccospheres were formed only of heterococcoliths (Plate 1A–D) with an average coccosphere diameter of 9.3 μm (6.9 – 11.9 μm). However, coccospheres formed only of holococcoliths (Plate 1D–F) and combination coccospheres of both heterococcoliths and holococcoliths (Plate 1G–I) were also observed. Combination coccospheres and holococcolith coccospheres were generally collapsed, thus cell size was not measured. Detached exothecal coccoliths of *S. bannockii* (Young et al., 2003) were also found in the samples. The abundance of holococcolith-heterococcolith combination coccospheres observed here confirm the decision by Cros et al. (2000) to describe *S. bannockii* as a single species with multiple life-cycle stages.

The holococcolith bearing diploid life-cycle stage of coccolithophores is generally poorly understood, although it has been suggested that multiple life cycle stages allows for adaptation to different nutrient conditions (Houdan et al., 2006) or to escape viral infection (Frada et al., 2008). That both life-cycle stages are present here suggest that the two stages may have similar ecologies and are both blooming at the same time, or perhaps that a bloom of *S. bannockii* HET is terminating and they are changing into their diploid holococcolith bearing stage to adapt to lower nutrient conditions (Houdan et al., 2006). Without further evidence, this question cannot be answered within this study.

5. Conclusion

A mixed bloom of *S. bannockii*, containing heterococcolith and holococcolith coccospheres, as well as holococcolith-heterococcolith combination coccospheres, was observed in multiple samples in the Bay of Biscay. This is the first time a bloom of *S. bannockii* has been reported, and provides clear confirmation that the life-cycle stage association described by Cros et al. (2000) is correct.

Acknowledgements

The study in which the samples were collected was funded by the European Project on Ocean Acidification (EPOCA) which received funding from the European Community's Seventh Framework Program (FP7/2007-2013) under grant agreement number 211384. This work was also made possible through funding from the European Union to the integrated project CARBOOCEAN (grant EVK2-CT-2000-00088) and through funding from the Department for Environment, Food and Rural Affairs (Defra) for the Defra pH project. C. J. Daniels was supported by a Natural Environmental Research Council studentship.

References

Balestra, B., Ziveri, P., Monechi, S. & Troelstra, S. 2004. Coccolithophorids from the Southeast Greenland Margin (Northern North Atlantic): Production, ecology and the surface sediment record. *Micropaleontology*, **50**(Suppl 1): 23-34, doi:10.2113/50.Suppl_1.23

Blackburn, S. & Cresswell, G. 1993. A coccolithophorid bloom in Jervis Bay, Australia. *Marine and Freshwater Research*, **44**(2): 253-260, doi:10.1071/MF9930253

Boeckel, B. & Baumann, K.H. 2008. Vertical and lateral variations in coccolithophore community structure across the subtropical frontal zone in the South Atlantic Ocean. *Marine Micropaleontology*, **67**(3-4): 255-273, doi:10.1016/j.marmicro.2008.01.014

Borsetti, A.M. & Cati, F. 1976. I1 Nannoplancton calcareo vivente nel Tirreno Centro-meridionale. Parte II. *Giornale di Geologia*, **40**(1): 209-240

Charalampopoulou, A., Poulton, A.J., Tyrrell, T. & Lucas, M.I. 2011. Irradiance and pH affect coccolithophore community composition on a transect between the North Sea and the Arctic Ocean. *Marine Ecology Progress Series*, **431**: 25-43, doi:10.3354/meps09140

Cros, L., Kleijne, A., Zeltner, A., Billard, C. & Young, J. 2000. New examples of holococcolith–heterococcolith combination coccospheres and their implications for coccolithophorid biology. *Marine Micropaleontology*, **39**(1): 1-34, doi:10.1016/S0377-8398(00)00010-4

Daniels, C.J., Poulton, A.J. & Sheward, R.M. 2014. Biogeochemical implications of comparative growth rates of *Emiliania huxleyi* and *Coccolithus* species. *Biogeosciences Discussions*, **11**: 10513-10536, doi:10.5194/bgd-11-10513-2014

Daniels, C.J., Tyrrell, T., Poulton, A.J. & Pettit, L. 2012. The influence of lithogenic material on particulate inorganic carbon measurements of coccolithophores in the Bay of Biscay. *Limnology and Oceanography*, **57**(1): 145-153, doi:10.4319/lo.2012.57.1.0145

Fiorini, S., Middelburg, J.J. & Gattuso, J.P. 2011. Effects of elevated CO_2 partial pressure and temperature on the coccolithophore *Syracosphaera pulchra*. *Aquatic Microbial Ecology*, **64**: 221-232, doi:10.3354/ame01520

Frada, M., Probert, I., Allen, M.J., Wilson, W.H. & De Vargas, C. 2008. The "Cheshire Cat" escape strategy of the coccolithophore *Emiliania huxleyi* in response to viral infection. *Proceedings of the National Academy of Sciences*, **105**(41): 15944-15949, doi:10.1073/pnas.0807707105

Geisen, M., Billard, C., Broerse, A.T.C., Cros, L., Probert, I. & Young, J.R. 2002. Life-cycle associations involving pairs of holococcolithophorid species: Intraspecific variation or cryptic speciation? *European Journal of Phycology*, **37**(4): 531-550, doi:10.1017} S0967026202003852

Harlay, J., Borges, A.V., Van Der Zee, C., Delille, B., Godoi, R.H.M., Schiettecatte, L.S., Roevros, N., Aerts, K., Lapernat, P.E., Rebreanu, L., Groom, S., Daro, M.H., Van Grieken, R. & Chou, L. 2010. Biogeochemical study of a coccolithophore bloom in the

northern Bay of Biscay (NE Atlantic Ocean) in june 2004. *Progress In Oceanography*, **86**(3–4): 317-336, doi:10.1016/j.pocean.2010.04.029

Harlay, J., Chou, L., De Bodt, C., Van Oostende, N., Piontek, J., Suykens, K., Engel, A., Sabbe, K., Groom, S. & Delille, B. 2011. Biogeochemistry and carbon mass balance of a coccolithophore bloom in the northern Bay of Biscay (June 2006). *Deep Sea Research Part I: Oceanographic Research Papers*, **58**(2): 111-127, doi:10.1016/j.dsr.2010.11.005

Houdan, A., Probert, I., Zatylny, C., Véron, B. & Billard, C. 2006. Ecology of oceanic coccolithophores. I. Nutritional preferences of the two stages in the life cycle of *Coccolithus braarudii* and *Calcidiscus leptoporus*. *Aquatic Microbial Ecology*, **44**(3): 291-301, doi:10.3354/ame044291

Milliman, J.D. 1980. Coccolithophorid production and sedimentation, Rockall Bank. *Deep Sea Research Part A. Oceanographic Research Papers*, **27**(11): 959-963, doi:10.1016/0198-0149(80)90007-2

Poulton, A.J., Charalampopoulou, A., Young, J.R., Tarran, G.A., Lucas, M.I. & Quartly, G.D. 2010. Coccolithophore dynamics in non-bloom conditions during late summer in the central Iceland Basin (July–August 2007). *Limnology and Oceanography*, **55**(4): 1601-1613, doi:10.4319/lo.2010.55.4.1601

Raitsos, D.E., Lavender, S.J., Pradhan, Y., Tyrrell, T., Reid, P.C. & Edwards, M. 2006. Coccolithophore bloom size variation in response to the regional environment of the subarctic North Atlantic. *Limnology and Oceanography*, **51**(5): 2122-2130, doi:10.4319/lo.2006.51.5.2122

Smith, H.E.K., Tyrrell, T., Charalampopoulou, A., Dumousseaud, C., Legge, O.J., Birchenough, S., Pettit, L.R., Garley, R., Hartman, S.E., Hartman, M.C., Sagoo, N., Daniels, C.J., Achterberg, E.P. & Hydes, D.J. 2012. Predominance of heavily calcified coccolithophores at low caco3 saturation during winter in the bay of biscay. *Proceedings of the National Academy of Sciences*, **109**(23): 8845-8849, doi:10.1073/pnas.1117508109

Tarran, G.A., Zubkov, M.V., Sleigh, M.A., Burkill, P.H. & Yallop, M. 2001. Microbial community structure and standing stocks in the NE Atlantic in June and July of 1996. *Deep Sea Research Part II: Topical Studies in Oceanography*, **48**(4–5): 963-985, doi:10.1016/S0967-0645(00)00104-1

Tyrrell, T. & Merico, A. 2004. *Emiliania huxleyi*: bloom observations and the conditions that induce them. *In*: H. R. Thierstein & J. R. Young (Eds.), *Coccolithophores: From Molecular Processes to Global Impact*. Springer-Verlag: 75-90.

Weeks, S.J., Pitcher, G.C. & Bernard, S. 2003. Satellite monitoring of the evolution of a coccolithophorid bloom in the Southern Benguela upwelling system. *Oceanography*, **17**(1): 83-89, doi:10.5670/oceanog.2004.70

Young, J.R., Geisen, M., Cros, L., Kleijne, A., Sprengel, C., Probert, I. & Ostergaard, J. 2003. A guide to extant coccolithophore taxonomy. *Journal of Nannoplankton Research Special Issue*, **1**: 1-132.

Young, J.R. & Ziveri, P. 2000. Calculation of coccolith volume and its use in calibration of carbonate flux estimates. *Deep Sea Research Part II*, **47**(9-11): 1679-1700, doi:10.1016/S0967-0645(00)00003-5.