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## HORIZONS

# Poleward expansion of the coccolithophore *Emiliana huxleyi*

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Coccolithophores are one of the most abundant eukaryotic phytoplankton in the oceans and are distinguished by their ability to build calcitic platelets (coccoliths). Of the numerous species, *Emiliana huxleyi* is considered one of the major calcifiers in the pelagic ocean. There is growing concern that increasing levels of CO<sub>2</sub> in the atmosphere and the subsequent acidification of the ocean may disrupt the production of coccoliths. Furthermore, any change in the global distribution and abundance of *E. huxleyi* relative to non-calcifying groups of phytoplankton (e.g. diatoms) will have important effects on the biogeochemical cycling of carbon and climatic feedbacks. We review different lines of evidence that suggest *E. huxleyi* is increasingly expanding its range into the polar oceans. These observations contribute to the debate on the climatic effects on natural coccolithophore populations. We postulate that *E. huxleyi* may be more sensitive to recent environmental changes such as increasing sea surface temperature and salinity than to changing ocean carbonate chemistry, partly because increased availability of CO<sub>2</sub>(aq) likely alleviates a carbon limitation for the inefficient Rubisco enzyme in these algae. Any potentially important climatic feedbacks of coccolithophores need a better knowledge of the mechanisms and rates of

adaptation by natural populations. As more data and modelling work become available, the real significance of this poleward expansion will become clear.

**KEYWORDS:** coccolithophores; biogeography; poles; geochemical cycling

## INTRODUCTION

Excluding physiological change and adaptation, the response of phytoplankton (and other organisms) to environmental changes can be manifested by alterations in their phenology and spatial distribution pattern (Hughes, 2000). Changes in the distribution pattern of marine phytoplankton are already evident (e.g. Beaugrand *et al.*, 2002; Thomas *et al.*, 2012). For example, the range of several species in the genus *Ceratium*, a common group of dinoflagellates, has expanded from their tropical and temperate regions into the recently warmer, more northern waters off Scotland and into the northern North Sea (Barnard *et al.*, 2004). Here, we examine the spatial distribution pattern of the cosmopolitan species *Emiliana huxleyi*, an important member of the coccolithophores.

Coccolithophores are a group of single-celled (2–20  $\mu\text{m}$  in diameter) marine algae, belonging to the division Haptophyta and they are one of the most important primary producing and calcifying microalgae (Winter *et al.*, 1994). *Emiliana huxleyi* is the most widely distributed and arguably the most abundant of approximately 200 extant coccolithophore species and at high concentrations it may be identified in satellite observations. Large blooms of *E. huxleyi* leave behind numerous detached coccoliths that impact the optical properties and mixed-layer ecological dynamics of the upper ocean (Brown and Yoder, 1994; Tyrrell *et al.*, 1999; Tynan *et al.*, 2001). Like other coccolithophores, *Emiliana huxleyi* is one of the major calcifiers in the open ocean (Iglesias-Rodríguez *et al.*, 2002) where its presence affects the partial pressure of  $\text{CO}_2$  in ambient surface waters through its influence on the ratio of inorganic to organic carbon (PIC:POC) in the water column (Shutler *et al.*, 2013). Calcification also decreases the alkalinity of the surface mixed-layer through export of calcite to the deep ocean and the sediments. As a consequence, any change in the global distribution and abundance of *E. huxleyi* relative to other non-calcifying groups of phytoplankton (e.g. diatoms) will have important effects on the biogeochemical cycling of carbon and climatic feedbacks (e.g. Cermeño *et al.*, 2008).

The coccoliths also allow blooms of *E. huxleyi* occupying the surface layer to be identified in visible satellite observations owing to their high ocean volume reflectance (Holligan *et al.*, 1993) and have their distribution

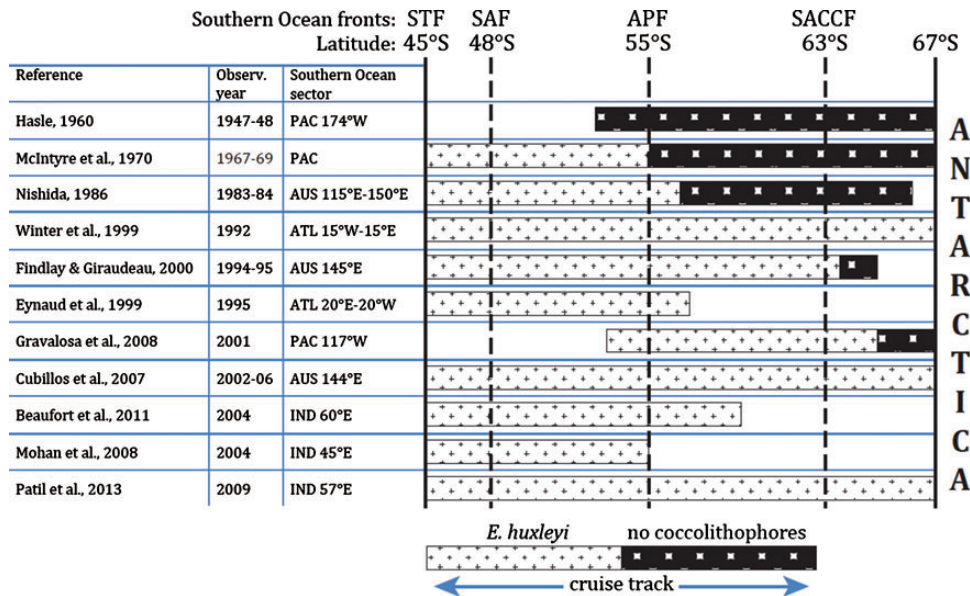
pattern mapped and monitored. *Emiliana huxleyi* blooms have been detected in imagery of the Advanced Very High Resolution Radiometer (AVHRR) and of the radiometrically more sensitive ocean colour sensors, such as Coastal Zone Color Scanner (CZCS), Sea-viewing Wide-field of View Sensor (SeaWiFS) and Moderate Resolution Imaging Spectroradiometer (MODIS) (Ackleson and Holligan, 1989; Brown and Yoder, 1993; Holligan *et al.*, 1993; Brown and Yoder, 1994; Iglesias-Rodríguez *et al.*, 2002; Smyth *et al.*, 2004; Balch *et al.*, 2011; Moore *et al.*, 2012). Their detection by satellites, however, is limited to approximately one attenuation depth in the water column and thus provides only a superficial and minimum estimate of the extent of the distribution of *E. huxleyi*, which typically exhibits a depth distribution concentrated at or immediately above the nutricline (Jordan and Winter, 2000; Beaufort *et al.*, 2008; Henderiks *et al.*, 2012).

Here, we present evidence from plankton samples, sediment traps, sediments and satellite imagery found in the literature that suggests that *E. huxleyi* is expanding its range poleward in both hemispheres over the last two decades. We offer potential biotic reasons behind this expansion, its possible implications and recommend areas of future research that will substantiate this recent movement.

## OBSERVATIONS

### *In situ* samples

Oceanic cruises have sampled 1–10 L of water in the photic zone (0–100 m) to specifically determine coccolithophore abundances since the early 1930s (Winter *et al.*, 1994), and ample evidence exists in the literature that the presence and abundance of *E. huxleyi* has increased in the polar oceans since the earliest systematic investigation started in the 1940s. No or few *E. huxleyi* existed in these waters then, but it is a common polar species now. In the southern hemisphere, oceanic sampling cruises from 1947 to 1986 found no evidence of *E. huxleyi* in the Antarctic Ocean south of the Polar Front (Antarctic convergence: approx.  $56^\circ\text{S}$ ), although this species was “the most widespread coccolithophorid in the sea” (Braarud, 1962) (Fig. 1). Two seminal papers on



**Fig. 1.** Schematic overview of the *Emiliana huxleyi* presence and absence from 11 oceanographic surveys in the Southern Ocean from 1947 to 2009. Southern Ocean fronts are indicated with their approximate summer (January–March) locations. Cruise year sector of the Southern Ocean, and associated reference are presented. Abbreviations: STF, Subtropical Convergence; SAF, Subantarctic Front; APF, Antarctic Polar Front; SACCF, southern Antarctic Circumpolar Current Front.

the distribution of coccolithophores in the Pacific Ocean are those of Hasle (Hasle, 1960), who investigated their distribution in 1947–48 along a transect at 174°W, and McIntyre *et al.* (McIntyre *et al.*, 1970), who assessed their distribution for the entire Pacific Ocean based on numerous oceanic cruises from 1967 to 1969. These papers concluded that *E. huxleyi* was absent south of the Antarctic convergence. A decade later, Nishida (Nishida, 1986) investigated coccolithophore distribution during the years 1983 and 1984 in the Australian sector of the Southern Ocean and also sought, but did not find, *E. huxleyi* south of the Antarctic convergence. Of course, this species may have been seasonally present without being identified in plankton samples because of its small size (typically 5 µm in diameter). If they were present in polar oceans, they were likely occurring in low concentrations.

Sampling suggests that sometime in the 1990s *E. huxleyi* expanded its range beyond the Polar Front in Antarctic waters where it is now seasonally abundant (Fig. 1). Winter *et al.* (Winter *et al.*, 1999) observed *E. huxleyi* along with 11 other coccolithophore species of subtropical origin from water samples taken across the Antarctic slope front (70°S) in the Weddell Sea in the austral autumn of 1992. The discovery of *E. huxleyi* and other coccolithophores that far south was completely unexpected. Since then, there have been numerous papers describing the presence of considerable concentrations (>10<sup>3</sup> cells L<sup>-1</sup>) of *E. huxleyi* in all sectors (Atlantic, Pacific, Indian and Australian) of the Antarctic Ocean

(summarized in Fig. 1). Findlay and Giraudeau (Findlay and Giraudeau, 2000) observed the species in the Australian sector of the Antarctic Ocean from 1994 to 1995. Eynaud *et al.* (Eynaud *et al.*, 1999) found numerous (>10<sup>2</sup> cells L<sup>-1</sup>) to abundant (>10<sup>3</sup> cells L<sup>-1</sup>) coccolithophores, including *E. huxleyi*, across the Antarctic Polar front. In this study, which took place in February and March 1995, coccolithophores were found at all stations and observed to be more abundant than diatoms except in the northern part of the Polar Frontal Zone and the Antarctic zone south of 51°30'S. Gravalosa *et al.* (Gravalosa *et al.*, 2008) collected large numbers of *E. huxleyi* in the Pacific sector during 2001 across the Polar Front up to the Antarctic Circumpolar Current Front (ACCF). Cubillos *et al.* (Cubillos *et al.*, 2007) observed significant abundances of *E. huxleyi* from 2001 to 2006 in the same area where previous researchers (Nishida, 1986; Findlay and Giraudeau, 2000) reported none, leading them to conclude that *E. huxleyi* had recently become abundant in these waters.

Mohan *et al.* (Mohan *et al.*, 2008) sampled in 2004 along a transect at 45°E in the Indian Ocean from 25°S to just across the Polar Front and found abundant *E. huxleyi* throughout. Conducting a survey on a similar transect (60°E) during the same year, Beaufort *et al.* (Beaufort *et al.*, 2011) found abundant numbers of *E. huxleyi* to 60°S across the Polar Front. Patil *et al.* (Patil *et al.*, 2013) identified abundant *E. huxleyi* from the eastern Pacific sector of the Southern Ocean across the

southern Antarctic Circumpolar Current Front (SACCF) to 66° S in the late Austral summer of 2010. Another study (Wright and van den Enden, 2000) applied an indirect method to determine coccolithophore concentrations using pigments that are representative of haptophytes, typically coccolithophores. It is highly likely that *E. huxleyi* was the dominant species where they performed their investigation (80 m depth between 80 and 150°E, from approximately 63°S to the sea-ice in the Austral summer of 1996). The accumulated evidence indicates that *E. huxleyi* is now a permanent member of the summer phytoplankton community of the Southern Ocean, including waters south of the Polar Front. This information requires that we update our understanding of their distribution pattern, as it is widely believed that no coccolithophores currently exist south of the Polar Front (Balch *et al.*, 2011).

A poleward expansion is also found in the northern hemisphere, where Scandinavian scientists have examined samples from waters around Norway since the 1940s (Halldal, 1953; Braarud *et al.*, 1958). They identified many diatoms and the coccolithophore *Coccolithus pelagicus* but found no blooms of *E. huxleyi* in the Nordic Seas in the 1940s, although blooms of *E. huxleyi* occurred every year since 1939 in the Oslo Fjord at about 60°N (Birkenes and Braarud, 1952). *Emiliania huxleyi* has recently been collected from the waters of the southern Barents Sea and from the high Arctic (80–81°N; Hegseth and Sundfjord, 2008; Solignac *et al.*, 2008; Charalampopoulou *et al.*, 2011). Sediment trap studies also show a general trend of an increasing contribution by calcifying plankton (or decreasing contribution by diatoms and other silicate plankton) across the North Atlantic during the 1990s (e.g. Deuser, 1996; Antia *et al.*, 2001). Down-core analyses of the alkenone concentration, organic biomarkers produced by *E. huxleyi* and a few related species within the Isochrysidales clade, deposited in coastal shelf sediments of the Bering Sea during the last 70 years, also indicate a major increase in the abundance of alkenone-producing coccolithophores since the 1970s that continues to the modern day (Harada *et al.*, 2012).

### Satellite imagery

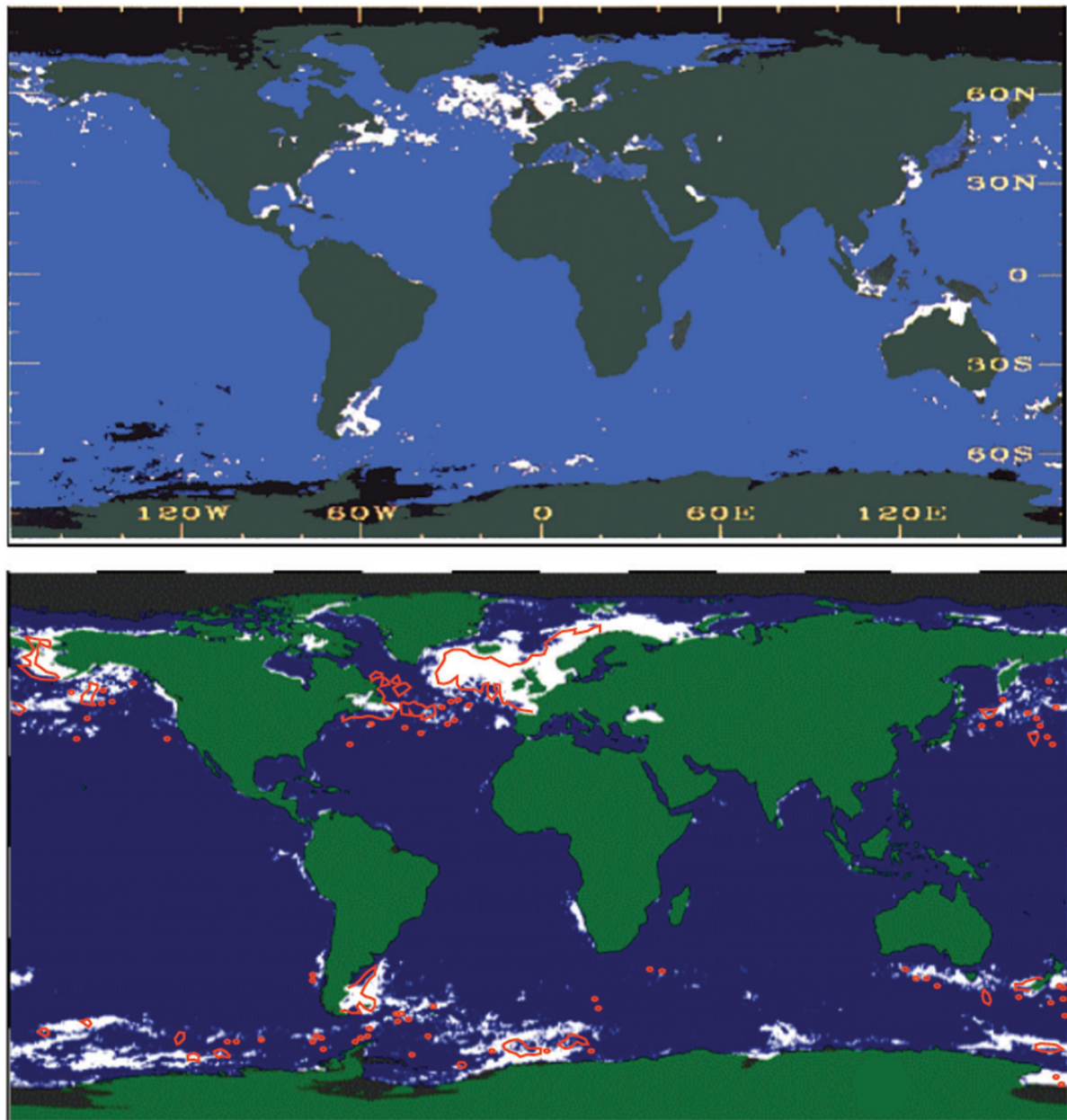
The *in situ* observations that demonstrate a poleward expansion of *E. huxleyi* are corroborated by satellite observations. The presence of high reflectance waters characteristic of *E. huxleyi* blooms in satellite imagery is clearly evident at high latitudes (>65°) in both the northern and southern hemispheres during the past decade or so where none was observed previously. In the northern hemisphere, Smyth *et al.* (Smyth *et al.*, 2004) examined AVHRR images of the Barents Sea dating from 1982 to

2002 and demonstrated the presence of coccolithophore blooms, most likely those of *E. huxleyi*, to be unambiguously present between 1989 and 1992, and from 1997 onwards, but saw no evidence of them in other years. (One other coccolithophore species in the region can, though infrequently, be detected in satellite imagery. A bloom of *Coccolithus pelagicus* was recorded in a continuously deployed sediment trap at 68°N north of Iceland (Olafsson *et al.*, 2000) that was also detected in contemporaneous SeaWiFS imagery (Brown, unpublished). *Gephyrocapsa oceanica* has also been detected from space (Blackburn and Cresswell, 1993), but is not found at polar latitudes.) Merico *et al.* (Merico *et al.*, 2003) inspected CZCS and AVHRR imagery dating from 1978 to 1996 for *E. huxleyi* blooms in the Bering Sea and found no evidence of their presence between 1978 and 1995. AVHRR images revealed that a small bloom was present in summer 1996. The following summer, in 1997, SeaWiFS revealed an *E. huxleyi* bloom of unprecedented extent in the Bering Sea (Vance *et al.*, 1998).

A poleward expansion of *E. huxleyi* blooms is also evident by comparing their global distribution pattern detected in CZCS imagery from the late 1970s /early 1980s (Fig. 2 top; Brown and Yoder, 1994) to that observed approximately 20 years later in SeaWiFS imagery (Fig. 2 bottom; Brown, unpublished). Superimposing the boundaries of *E. huxleyi* blooms detected in CZCS on blooms identified in SeaWiFS imagery from 1997 to 2007 illustrates the apparent increase in areal extent and more poleward position of these blooms in the latter period. Both maps were generated similarly by grouping pixels of weekly global composites of this imagery into coccolithophore bloom and non-bloom classes using a supervised, multispectral algorithm based upon mean remote sensing reflectances (Brown and Yoder, 1994; Iglesias-Rodríguez *et al.*, 2002). Annual and climatological composites of bloom presence were created by combining classified images so that the location of all classified blooms detected during the defined period are displayed (Fig. 2).

The attribution of the difference in distribution between satellite detected blooms in CZCS and SeaWiFS (and MODIS) is difficult because of changes in sensor characteristics, radiometric sensitivity and imagery coverage. Imagery coverage, for example, varied temporally and spatially during the proof-of-concept CZCS mission, with the frequency of coverage, which was concentrated in coastal regions at mid latitudes of the northern hemisphere, highest in the first full 3 years (1979–1981) (McClain *et al.*, 1990), compared with the essentially constant frequency of coverage by the dedicated ocean colour SeaWiFS mission (McClain *et al.*, 2004), and thus will bias the resulting distribution pattern of *E. huxleyi*





**Fig. 2.** Climatological composites of classified coccolithophore blooms detected in (top) CZCS imagery from November 1978 to June 1986 (from Brown and Yoder, 1994) and (bottom) SeaWiFS imagery from October 1997 to September 2007 (Brown, unpublished). The maximum spatial extent of blooms detected during the period is displayed in the composites. The coccolithophore bloom class is in white, the non-coccolithophore bloom in blue, land in green, lack of image coverage in black. The red outline indicates the spatial extent of classified coccolithophore blooms detected during CZCS.

detected between the two ocean colour sensors. Also, several other oceanic conditions, such as suspended calcareous sediments and diatom frustules, mimic the spectral characteristics of *E. huxleyi* blooms in satellite imagery and may be incorrectly classified as blooms. Such complications, however, are principally limited to nearshore, shallow waters. Yet the detection of blooms at similar locations in polar regions in recent ocean colour and

AVHRR imagery, which is radiometrically less sensitive than the former, gives credence to our contention that *E. huxleyi* blooms are indeed expanding poleward. The presence of the “Great Calcite Belt”, a region of elevated concentrations between the Subantarctic Front and Polar Front in the Southern Ocean during the austral summer (Balch *et al.*, 2005, 2011), and consisting of coccoliths, also confirms the presence of coccolithophores, including

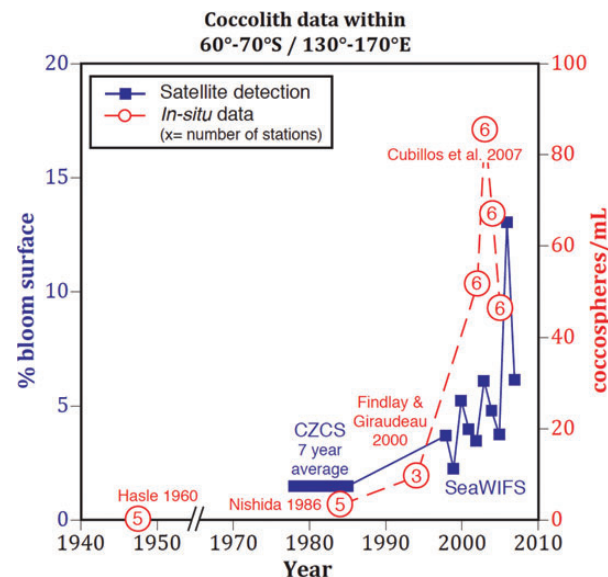
*E. huxleyi*, in high latitude, polar waters as observed in shipboard collected samples.

Furthermore, plotting the spatial extent of their blooms detected during CZCS and SeaWiFS (1997–2007) as a percentage of the surface area in the region located between 30–70°S and 130–140°E, shows a correspondence with *in situ* observations of *E. huxleyi* coccosphere abundance over the same period in the Southern Ocean (Fig. 3). The surface areas of satellite-detected blooms were calculated from the CZCS mission (Fig. 2 top; taken as a 7-year average) and annual composites of SeaWiFS (not shown), respectively, by multiplying pixel area by the frequency of bloom pixels. Both satellite and *in situ* observations show an increase in the 1990s, suggesting that bloom size and intensity increased simultaneously in this region.

Given these *in situ* and remote observations, suggesting a poleward expansion of *E. huxleyi*, are there any plausible biological reasons to support this movement?

## CONTRIBUTING FACTORS

*Emiliana huxleyi* is certainly unique among the coccolithophores. It is an evolutionarily young species, first occurring in Pleistocene fossil records ~290 000 years BP



**Fig. 3.** Percentage of surface area of classified *Emiliana huxleyi* blooms in CZCS (1978–86) (from Brown and Yoder, 1994) and SeaWiFS (1997–2007) (from Brown, unpublished) in the region 30°–70°S / 130°–170°E (in blue) and *in situ* observations of *E. huxleyi* abundance in the same region (in red). Red circles represent the average abundance (in coccospheres/mL), as reported for multiple stations (number indicated) in the mentioned literature sources. Hasle (Hasle, 1960) investigated five stations in 1947–48, and she concluded that *E. huxleyi* was absent.

(Raffi *et al.*, 2006), descended from a lineage that has been phylogenetically separated from most other extant coccolithophores for ~195 million years (Medlin *et al.*, 2008) and it rose rapidly to global dominance (Thierstein *et al.*, 1977). Its ability to adapt to a broad range of environments and maintain extensive blooms in nearly every marine biome is likely due to its extensive genetic (Iglesias-Rodríguez *et al.*, 2006; Read *et al.*, 2013) and ecophenotypic plasticity (Langer *et al.*, 2009) that should give it a competitive advantage. Furthermore, it is the only coccolithophore species with a non-calcifying haploid stage and an occasional naked diploid stage (Paasche, 2002). Sampling of polar waters reveals that only a few distinct morphotypes of *E. huxleyi* are leading the polar “migration” (Cubillos *et al.*, 2007) that are thus seemingly best adapted to the changing polar habitats. Moreover, the morphotypes encountered in the Southern Ocean are genetically distinct from each other (Cook *et al.*, 2011), suggesting that genetic diversity underpins their physiological plasticity and adaptations.

One environmental change receiving much attention is ocean acidification (OA), which is especially acute in polar regions (Orr *et al.*, 2005). The effects of OA on *E. huxleyi* calcification are still hotly debated primarily because both laboratory (e.g. Riebesell *et al.*, 2000 vs. Iglesias-Rodríguez *et al.*, 2008) and observational data (e.g. Beaufort *et al.*, 2011 vs. Smith *et al.*, 2012) give contradictory results. The relationship between *E. huxleyi* coccolith dissolution/calcification is non-linear and complicated not least by its extensive morpho/genotypic variability. Recent culture experiments suggest that some strains of *E. huxleyi* could withstand changes in pH much better than others (Iglesias-Rodríguez *et al.*, 2008; Langer *et al.*, 2009). Why this is so is unclear, but one possibility is that photosynthesis in *E. huxleyi* is more efficient at higher levels of CO<sub>2</sub>. The carbon fixing Rubisco enzyme is inefficient at low levels of CO<sub>2</sub> within all algae (Young *et al.*, 2012). But diatoms (Giordano *et al.*, 2005) and other coccolithophore species (Moolna and Rickaby, 2012) may be better adapted to low CO<sub>2</sub> due to more efficient carbon acquisition than *E. huxleyi* (Rost and Riebesell, 2004). Thus *E. huxleyi* may become more competitive as CO<sub>2</sub> rises.

The expansion of *E. huxleyi* into polar waters may be a result of either shifts in water masses in which *E. huxleyi* is already established or changing water temperature and chemistry that provides improved conditions towards the poles for some of its genotypes. Certainly, there could be different regional and hemispheric explanations. Mesoscale eddies in the southern polar regions may bring nutrients favourable to *E. huxleyi* across the polar fronts (Winter *et al.*, 1999; Fyfe *et al.*, 2007; Kahru *et al.*, 2007). Eddies may bring nutrients such as NH<sub>4</sub> which

*E. huxleyi* uses as an additional source of nitrogen (Lefebvre *et al.*, 2012) but which is known to inhibit NO<sub>3</sub> uptake by other phytoplankton at concentrations >4 µmol/L (Dugdale *et al.*, 2007). In the past few decades, such cross-frontal eddy activity has increased in response to shifting winds associated with the Southern Annular Mode (SAM) (Meredith *et al.*, 2004). Climate models show that the SAM is responding to increasing greenhouse gases and Antarctic ozone depletion (Shindell and Schmidt, 2004). In the northern Polar Regions increasingly ice-free conditions in summer allow blooms of *E. huxleyi* into the Arctic Sea through open straits (Rigor and Wallace, 2004). A shift in sub-surface circumpolar currents due to earlier ice melt is thought to be responsible for the obvious change in phytoplankton composition in the northern Barents Sea (Hegseth and Sundfjord, 2008; Solignac *et al.*, 2008). The melting of sea ice may precondition the surface layer for *E. huxleyi* blooms by reducing salinity, or increasing stratification (Smyth *et al.*, 2004). The geological record suggests that *E. huxleyi* was also present in the Arctic during diminished sea-ice conditions of past interglacial times (Backman *et al.*, 2009). The rising surface temperature of the high latitudes oceans also has important consequences for the migration of phytoplankton (Thomas *et al.*, 2012) and could provide a simpler explanation for the recent migration of *E. huxleyi* into the polar waters. Another possible reason is that the growing season is becoming longer, leading to more oligotrophic conditions (low to intermediate nutrient concentrations) that favour coccolithophores.

## POSSIBLE IMPLICATIONS

Given the complexity of Polar Regions and the limitations of current modelling, it is difficult to predict the implications of the expanded range of *E. huxleyi*. The mere observation of a poleward movement of this species, however, should raise concern about a change in the polar marine ecosystem. The impact of abundant *E. huxleyi* in higher latitudes should cause an observable change in the marine food web as any shift in phytoplankton assemblages will likely result in a change in grazing communities and force shifts in the type and success of grazers, including fish, birds and marine mammals (Napp and Hunt, 2001; Tynan *et al.*, 2001).

Furthermore, highly abundant eukaryotic phytoplankton, including coccolithophores, provide the most efficient export of carbon to the deep ocean through photosynthetic fixation of inorganic carbon into organic matter (the so-called biological pump). However, the overall biogeochemical effect of a phytoplankton bloom is different depending on whether calcifying or non-

calcifying phytoplankton dominate the bloom. Depending on the community photosynthesis to calcification ratio, a bloom of calcifying *E. huxleyi* can cause a decrease of pCO<sub>2</sub>, while non-calcifying algae consuming the same amount of inorganic nutrients would cause an even larger decrease in pCO<sub>2</sub>. A recent mesocosm experiment that sampled through the full bloom cycle of *E. huxleyi* showed a distinct decreasing trend in pCO<sub>2</sub>, suggesting that the overall balance of the bloom was towards a sink for atmospheric CO<sub>2</sub> (Delille *et al.*, 2005). Indeed, a modelling study (Barker *et al.*, 2006) on bloom-forming coccolithophores in the geological past showed that they can provide a controlling feedback to atmospheric CO<sub>2</sub>.

Blooms of *E. huxleyi* also significantly change the chemistry of the ocean in their vicinity. This is observed today in non-polar areas, where calcification within coccolithophore blooms significantly decreases alkalinity by as much as -2.5% at the surface and exports CO<sub>2</sub> to the atmosphere (Holligan *et al.*, 1993). Hence, an extension of the bloom forming *E. huxleyi* to the polar regions may pump additional alkalinity from surface water to the deep ocean.

## CONCLUSIONS AND RECOMMENDATIONS FOR FUTURE WORK

The extensive *in situ* and satellite observations are indications that *E. huxleyi* is expanding its range into polar waters. Further research needs to determine whether the Arctic growing season has become longer, leading to more oligotrophic conditions, which may favour coccolithophores. Whether the range of the satellite-detected blooms has simply shifted polewards or has expanded latitudinally, and if bloom intensity, not just their abundance, has decreased or increased over time, awaits future *in situ* monitoring and improved satellite techniques. This could be accomplished by comparing where the highest values of coccolithophore algorithms occur in the two sensors. The sedimentary record of alkenones in high sedimentation rate areas in polar regions may also be an excellent way to detect changes in the abundance of *E. huxleyi* and its close relatives. In any case, the more recent observations of abundant *E. huxleyi* in polar water are undeniable. We need a better understanding of the mechanisms and rates of adaptation of natural populations to determine any potential climate feedback of coccolithophores. Understanding why *E. huxleyi* has such a high genetic diversity (Read *et al.*, 2013) and exploring its physiologic plasticity (Langer *et al.*, 2009) will be key aspects in attaining this crucial knowledge.



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