RESEARCH PAPER

THE PHENOMENON OF *EMILIANIA HUXLEYI* IN ASPECTS OF GLOBAL CLIMATE AND THE ECOLOGY OF THE WORLD OCEAN

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ABSTRACT. *Emiliania huxleyi* (Lohmann) evolved from the genus *Gephyrocapsa* Kamptner (Prymneosiophyceae) of the coccolithophore family Naëlaerhadaceae. Over the past 100 thousand years *E. huxleyi* has acquired the status of the most ecologically predominant coccolithophore due to its remarkable adaptability to a variety of environmental conditions and interspecific competitiveness. *E. huxleyi* plays an important role in both the marine carbon system and carbon cycling between the atmosphere and ocean due to its ability to produce organic and inorganic carbon as well as to form massive blooms throughout the world ocean. This study examines both older information and recent findings to shed light on the current tendencies in the two-way interactions between *E. huxleyi* blooms and the immediate and global environment under conditions of climate change. The assembled knowledge has emerged from laboratory and mesocosm instrumental investigations, retrievals of satellite remote sensing data, machine learning/statistical analyses, and numerical simulations. Special attention is given to both the quantitative data reported over the last two decades on such interactions, and the only very recently appearing mid-term projections of *E. huxleyi* bloom dynamics across the world ocean. These blooms strongly affect the atmosphere and ocean carbon cycles. They reduce CO_2 fluxes from by ~50% to ~150% as is documented for the North Atlantic, and on the global scale release particulate inorganic carbon as calcium calcite in the amounts assessed at 0.4 to 4.8 PgC/yr. At the same time, they are also sensitive to the atmospheric and oceanic state. This results in *E. huxleyi* blooms having an increased impact on the environment in response to ongoing global warming.

KEYWORDS: coccolithophores, *Emiliania huxleyi*, cell morphology, genetic diversity, physiology, blooms, environment and forward and feedback interactions, climate change and future scenarios

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INTRODUCTION

A coccolithophore *Emiliania huxleyi* (Lohmann) W. W. Hay et H. P. Mohler (Prymneosiophyceae) is known as the most productive calcifying organism on Earth (Paasche 2002; Tyrrell and Young 2009). This alga is found to be an important player in the processes that form the marine carbon system and the CO_2 partitioning between the atmosphere and the uppermost layer of the ocean. Furthermore, *E. huxleyi* contribute to marine sulphur cycles by producing a precursor of dimethylsulphide (DMS), the latter being a precursor for the generation of maritime aerosol. These properties are particularly consequential as *E. huxleyi* is able to form extensive and intensive blooms throughout the world ocean. This gives *E. huxleyi* an important role in marine biogeochemistry, marine ecology and the climate system.

This explains much of the interest in this algal species that has made it one of the best-studied marine organisms, not least due to the ease of growing *E. huxleyi* under laboratory conditions. To date, several reviews on *E. huxleyi* have been published covering a wide range of issues related to this alga (Paasche 2002; Rost and Riebesell 2004; Tyrrell and Merico 2004).

The present review was prompted by many new studies that have appeared since then. These recent works have shed more light on, amongst other things, cell morphology and intracellular biochemistry, including the intrinsic mechanisms of calcification in conjunction with organic matter production. The growing data from satellite observations that began in 1997–1998 enabled regional and worldwide quantitative assessments of the interannual dynamics of bloom extent; the associated production of particulate inorganic carbon; elevations in dissolved CO_2; and the enhancement of CO_2 partial pressure over *E. huxleyi* bloom areas. New insights have been reported on the two-way interactions between these algae communities and the environment in the context of increasing atmospheric CO_2 concentrations, global warming, and ocean acidification.

Spaceborne data have also contributed to a better (but still incomplete) understanding of the environmental forcing factors that determine the onset, duration, and intensity of *E. huxleyi* blooms. There have also been tentative quantitative assessments of how bloom dynamics may change in the future in response to ongoing climate change.

No single review is able to cover all aspects of the knowledge that has emerged on *E. huxleyi*. In this manuscript we chose to concentrate on the ecology of this alga and its influence on the atmosphere and ocean, as well as the vice versa influence on this alga of the changing climatic conditions of the recent past and near future. Nonetheless, our review explores some «old knowledge», since the basic accomplishments in *E. huxleyi*-related research continue to be fundamental for our understanding of the phenomena related to this remarkable marine organism.

A HISTORIC OVERVIEW OF ORIGIN AND DEVELOPMENT

The coccolithophore family Naëlaerhadaceae has been the most plentiful taxon of coccolithophore communities (Raffi et al. 2006) for the last 20 million years, with *Gephyrocapsa oceanica* Kamptner being predominant. Some 270.000 years ago a new species, *Emiliania huxleyi*, evolved and has become differentiated from the older *G. oceanica* (Thierstein et al. 1977). Some 200.000 years after this differentiation *E. huxleyi* has replaced G. oceanica as the most ecologically prominent coccolithophore. This is due to its phenomenal ability for adaptation to a wide range of environmental conditions and a remarkable interspecific competitiveness. Presently, the cell number of *E. huxleyi* in coccolithophore communities across the world ocean accounts for 30% to 50%, and up to 100% at subpolar latitudes (Mohan et al. 2008).

CELL MORPHOLOGY

Like all coccolithophores, *E. huxleyi* is characterized by the haplodiplontic and heteromorphic life cycle encompassing diploid and haploid phases (Green et al. 1996; Frada et al. 2012). The former incorporates both a coccolith-bearing non-motile phase (formation of calcified cells), and a non-calcified non-motile phase (formation of naked cells). The haploid phase is a non-calcified biflagellated one (formation, presumably because of mutation, of organic scales bound to the plasmalemma). Growing diploid populations eventually transform into a haploid cell stage (Read et al. 2013). In the diploid phase, *E. huxleyi* cells bearing calcified coccoliths often form extensive blooms.

Diploid cells of *E. huxleyi* are composed of an inner organic-rich matter covered by interlocking calcium carbonate scales/coccoliths forming an exoskeleton, whose morphology largely reflects the genetic variability of the gene. *E. huxleyi* has three well-characterized calcification morphotypes: A, B, and C. (Paasche 2002). There are additional morphological variations within each coccolith morphotype. A and B are the two major coccolith morphotypes of *E. huxleyi*. Additionally, the types B/C, R, and corona are recognized (Hagino et al. 2011).

E. huxleyi morphotypes are distinctly ecotypes. They are responsive to such environmental drivers as water temperature, salinity, light and nutrient availability that together determine their biogeography (Rigual-Hernandez et al. 2020). As Krumhardt et al. (2017) reviewed, morphotype A is a widespread «warm water» type inhabiting waters from the subtropics to subpolar. It predominates in the North Atlantic south of 60°N, south of the South Subtropical Front but north of the Subantarctic Front, and in subtropical gyres. Morphotypes B/C and C (which are generally classified as B/C morphotype) are a «cold-water» type native to high latitudes (North Atlantic at latitudes >60°N and south of the Subantarctic Front) as well as in upwelling oceanic regions. They are tolerant to high pCO_2, and are less calcified than morphotype A. There is also an over-calcified group of *E. huxleyi* composed of A-over-calcified and morphotype R. Morphotype R is found in coastal New Zealand and a few other productive coastal waters, whereas A-over-calcified inhabits parts of the Southern Ocean (Poulton et al. 2011). The mass of coccoliths of Type A, overcalcified A, and B do not differ systematically, and hence there is no systematic relationship between relative abundance of a morphotype and the overall calcite production of *E. huxleyi* (Johnsen and Bollmann 2020).

Synthesized intracellularly, coccoliths are eventually extruded to the cell surface until a complete coccosphere covering is formed. Normally, *E. huxleyi* build up a complete single layer (10-15 coccoliths are needed to form a complete coccosphere (Paasche 2002)), but under strained conditions, ene overproduces coccoliths to form a multi-layer cover up to 4 layers thick, made up of over one hundred coccoliths (Balch et al. 1993). Eventually, the excessively overlaid cell becomes unstable and begins losing some upper-layer coccoliths into the surrounding water well before the end of the life cycle when the cell becomes totally naked. The mechanism of coccolith formation and extrusion out of the cell's body is not yet fully understood (Brownlee et al. 2015).

Moreover, even the role of coccoliths still remains uncertain as many possible options have been envisaged (Müller 2019). In terms of the ecologically biotic function, *E. huxleyi* cells might have evolved coccoliths to protect them from grazing by zooplankton (although this is contested by Strom et al. (2020)), as well as to reduce the risk of penetration of viruses and bacteria into the cell. It has also been conjected that, by increasing the cell's weight, the coccoliths raise the rate of diurnal downward movements of cells within the euphotic zone and thus elevate the rate of nutrient uptake by the cell due to its more intense washing. In light of the well-established resistance of *E. huxleyi* to photoinhibition, it appears possible that its carbonate cover protects the cell against very high light intensities by dissipating impinging light (Johnsen and Bollmann 2020). Also, a cellular biochemical aspect may be involved through the carbon concentration mechanism for photosynthesis, phosphorus metabolism (avoidance of intracellular precipitation and detoxication), and the maintenance of a balance between high external and low intracellular Ca concentration (Vargas et al. 2007). In any case, the diversity of coccolith morphology makes it likely that coccoliths have evolved to perform a range of functions.

The remarkable omnipresence of *E. huxleyi* in the world ocean is explained by versatile ecotypes/strains of this alga arising from genetic variability and genomic organization. All *E. huxleyi* morphospecies have a common «core-genome» incorporating the genes responsible for vital functioning of the cell and defining to a major degree the fundamental features of the species. This core genome is complemented with some specific genes distributed between strains that condition the environmental fitness of *E. huxleyi* strains/ecotypes. As such, a pan-genome ensures the phenomenon of ecological competitiveness/cosmopolitism of this alga (Read et al. 2013; von Dassow et al. 2015), and ostensibly implies that such a high degree of genetic diversity translates into a spectrum of ecological functions (Iglesias-Rodriguez et al. 2006).

This genetic flexibility is the key to the ecological success of *E. huxleyi*. It imparts the ability to endure high radiance levels and low metal (especially Fe) availability (Miller et al. 1991); tolerate nutrient (nitrogen) paucity (Kaffes et al. 2010); possess efficient phosphate uptake and an organically bound phosphate scavenging system (Riegman et al. 2000); and provides immunity to grazing by some microzooplankton species (Merico et al. 2004). These capacities are further complemented by the ability of *E. huxleyi* to grow in marine environments with a wide range of water temperature, salinity, vertical mixing/stratification, and extremely high and low (even under-ice) illumination conditions (Balch et al. 2014; Silkin 2017; Nissen et al. 2018; Kondrik et al. 2019).

CELL intracellular biochemistry related to calcification

Two basic biochemical reactions of photosynthesis and calcification (eq. 1) occur in *E. huxleyi* cells:

$$\begin{gathered} 6CO_2 + 12H_2O \rightarrow C_6H_{12}O_6 + 6O_6 + H_2O \\ Ca^{2+} + 2HCO_3^- \rightarrow CaCO_3 + CO_2 + H_2O \end{gathered} \quad (1)$$

Investigation of intracellular calcification indicated that the conditioning role in this process is played by the expression of the *AEL1, CAX3* and *ATPVc′/c* genes (Mackinder et al. 2011). Both reactions proceed within their own compartments that are spatially separated. Nonetheless, there is energetic coupling of the two reactions. It has been claimed that this coupling is unidirectional: that the calcification reaction takes up energy from photosynthesis as both reactions proceed during day-time. Unlike some other coccolithophores (*e.g., Coccolithus braarudii* (K. R. Gaarder) K. Baumann, M. Cachao, J. R. Young and M. Geisen in the diploid phase), the photosynthesis reaction in *E. huxleyi* cells does not necessarily need the intracellular CO_2 and\or protons produced by calcification [the latter for conversion of $2HCO^-_3$ to CO_2] (Brownlee and Taylor 2004; Walker et al. 2018). Moreover, it is shown that calcification – an energy demanding process for a cell - plays photoprotective roles when the cell is exposed to excessively high solar radiation (Xu and Gao 2012).

Thus, CO_2 for photosynthesis is principally of external origin, similarly to $2HCO^-_3$ (Balch et al. 2014). CO_2 is transported into the cell by diffusion from ambient water, which in turn comes from the dissolution of atmospheric CO_2 into water:

$$CO_2 + H_2O \leftrightarrow H_2CO_3 \leftrightarrow 2HCO_3^- + H^+ \leftrightarrow CO_3^{2-} + 2H^+ \quad (2)$$

Although the bulk calcification process (i.e., precipitation of $CaCO_3$ from Ca^{2+} and CO_3^{2-}) is well-established, the intricate intracellular transport routes remain unclear. Thus, it is presently assumed that most likely Ca^{2+} enters the cell via Ca^{2+} permeable channels in the plasma membrane (Brownlee and Taylor 2004) with further accumulation in the Golgi. This question of how the transport routes work is of fundamental importance because it determines the kinetic rate of the entire process. So, while it remains unanswered, so too do questions about the associated cellular machinery at a more intimate level. Meanwhile, the precise understanding of Ca^{2+} homeostasis is important for a more precise prediction of the world ocean response to increasing global atmospheric CO_2 concentrations, especially in light of the fact that calcification triggers the expression of specific genes within the pan-genome that regulate metabolic processes in response to environmental conditions (Section 3).

Biochemical role in carbon cycling and emissions of organo-phosphorus compounds and methane: machinery and consequences

The flow of atmospheric CO_2 into the surface ocean is determined by the fixation of dissolved CO_2 via photosynthesis (Eq. 1), followed by the downward transport of particulate organic carbon (the so-called carbon pump). The absorption of atmospheric CO_2 into the ocean can be further enhanced by the drawdown of sea water alkalinity i.e., the number of negative ions formed through dissociation of carbonic acid (Eq. 2) due to the removal of HCO^-_3 from surface water. This latter process is hugely important within *E. huxleyi* blooms due to the production of $CaCO_3$ via calcification i.e., subsequent settling of coccoliths (calcite) down into the deep sea (known as the carbonate pump). At the same time, the CO_2 produced during calcification permeates through the membrane, goes out into the surrounding water, and replenishes the pool of dissolved CO_2 within the euphotic zone (Rost and Riebesell 2004). Therefore, calcification can result in either reduction or even inversion of CO_2 fluxes at the ocean-atmosphere interface within the bloom area.

The natural organic surface coating on *E. huxleyi* cells (Godoi et al. 2008) facilitates the dissolution of calcite even in calcium carbonate oversaturated waters. As calcite solubility increases with decreasing temperature (Alekin 1966), the dissociation of $CaCO_3$ at depth eventually initiates the upward transport of dissociation products, thus closing the loop of carbon turnover in the ocean. The dissociation of $CaCO_3$ is especially important below the lysocline where the pressure effect dramatically increases the calcite dissolution.

E. huxleyi blooms are associated with emissions of the volatile compound dimethylsulfide (DMS) (Malin and Steinke 2004), like the blooms of some other algae (e.g., dinoflagellates and several colony-forming species, e.g., *Phaeocystis*). When emitted to the atmosphere, DMS can affect cloud formation, which is consequential for the global climate.

The present knowledge (Vogt and Liss 2010) suggests that DMS $[(H_3C)_2S]$ in seawater is produced (along with acrylate $[H_2CHCOO^-]$ and a proton) owing to extracellular cleavage of dimethylsulphoniopropionate $[(CH_2)_2 + SCH_2CH_2COO^-]$ (abbreviation DMSP) rather than direct excretion by *E. huxleyi* cells (Eq. 3):

$$\begin{gathered} \left[(CH_2)_2 + SCH_2CH_2COO^-\right](DMSP - lyase)/(\text{bacteria and} \\ \text{algae}) \rightarrow \left[(H_3C)_2 S\right] + \left[H_2CHCOO^-\right] + H^+ \end{gathered} \quad (3)$$

The above DMSP breakdown reaction is initiated by either dimethypropiothetin dethiomethylase (DMSP-lyase) or bacteria (attached or symbiotic). The triggering mechanism of reaction (3) in the case of healthy *E. huxleyi* cell is zooplankton grazing. However, it seems that microzooplankton do not themselves convert DMSP to DSM but rather spur the activation of algal DMSP-lyase and microbial enzymic intervention. The bacterial degradation processes become the most important DMSP-lyase activation pathway in the senescence phase of the life-cycle of *E. huxleyi* cells. At this stage of the life-cycle, viral infection is thought to play an important role as the virus lysis eventually results in liberation of the cell's content into the water, making it easy prey for bacteria (Evans et al. 2007). Alcolombri et al. (2015) have identified the DMS releasing gene in *E. huxleyi*: it proved to be Alma 1 – a tetrameric redox-sensitive enzyme belonging to the gene family common for the major phytoplankton taxa.

The physiological role of DMSP is thought to be multifaceted cell protection: osmoprotection (counteract excessive water salinity), cryo-protection (anti-freezing), and antioxidantant action (scavenging of OH^- radicals) (Vogt and Liss 2010). DMS emissions from the ocean have been found to be within 17-34$TgSyr^{-1}$, which accounts for about 50% of the total global sulfur entering the atmosphere annually (Lana et al. 2011).

Along with CO_2, CH_4 is one of the main greenhouse gases. There is unambiguous evidence for production of methane (CH_4) by widespread haptophytes such as Phaeocystis globosa, Chrysochromulina sp., and *E. huxleyi* (Klintzsch et al. 2019). Remarkably, this process occurs even in marine waters oversaturated with O_2, i.e., under conditions that do not favor methanogenesis. Nonetheless, a 5%-75% oversaturation of CH_4 within *E. huxleyi* bloom areas has been documented (Lenhart et al. 2016). It is conjected that CH_4 is produced by *E. huxleyi* over the entire life-cycle, including the senescence phase, so that this process is part of its normal metabolism. Indeed, the data obtained indicate that bicarbonate (taken up by the algae via autotrophic C fixation) is the principle inorganic carbon precursor of CH_4 produced in algae, while the main organic precursor of CH_4 is methionine (Met) [$C_5H_{11}NO_2S$] – a methyl group donor. Algae-derived DMSO can also act as a precursor of CH_4 in oxic seawater (Althoff et al. 2014). Cumulative (anthropogenic and natural) emissions of CH_4 are assessed at 500-600$Tgyr^{-1}$ (Lenhart et al. 2016), but the global contribution solely due to coccolithophores remains moot as other algal species, such as dinoflagellates, are also very productive in this regard.

E. huxleyi bloom CO_2-related impacts on the environment

Carbonate counter pump

Satellite-borne estimations covering the period 1998–2019 showed that *E. huxleyi* blooms in Subarctic and Arctic seas as well as in the Black Sea resulted in the release of ten to several hundreds of kilotons of inorganic carbon (PIC) into surface water in the form of $CaCO_3$. In the Barents Sea, the released PIC content varied between ~100 kt and 250-300 kt, whereas in the Bering Sea the PIC content was as high as 500 kt during two periods of exceptional activity (Kondrik et al. 2017). Although the reported estimates of annual PIC production on a global scale vary widely, they are nevertheless very high: ~ 0.4 to 1.8 $PgCyr^{-1}$ (Balch et al. 2016).

Increment of CO_2 partial pressure within blooms and in the atmospheric column over them

There is ample evidence that the release of PIC was accompanied by a significant increase in CO_2 partial pressure (ΔpCO_2) within the bloom area: between 1998 and 2016, the mean and maximum values of the ratio $\Delta pCO_2/(\Delta pCO_2)_{background}$, varied in the range ~ (20-40)%, and ~ (30-60)%, respectively. The highest numbers were registered in the Bering and Barents seas (Kondrik et al. 2018; Kondrik et al 2019).

The recent quantitative assessments of *E. huxleyi* bloom influence on surface water CO_2 partial pressure (pCO_2) showed that in the North, Norwegian, Greenland, Barents, Bering and Black seas *E. huxleyi* blooms accounted for a very significant pCO_2 enhancement (ΔpCO_2).

For the regions of prevalent coccolithophore (*E. huxleyi*) blooms in the North Atlantic, Shutler et al. (2013) found that the average reduction in the monthly air-water CO_2 flux could reach 55%, while the maximum reduction within the time period 1998–2007 was as high as 155%.

The impact of *E. huxleyi* blooms on CO_2 exchange at the air-sea surface interface was quantified from satellite OCO-2 data: the numerous remote sensing case studies over the aforementioned North Atlantic seas as well as in the Barents and Black seas proved that $(\Delta pCO_2)_{atm}$ could reach 2-3 ppm (Kondrik et al. 2019, Morozov et al. 2019). Such increments constitute ~ 0.5% of the present mean pCO_2 in the atmosphere (Dlugokencky 2016) and is comparable to the annual increase in global-mean atmospheric CO_2. These data give evidence that *E. huxleyi* blooms can significantly weaken marine carbon sinks on a global scale.

Physiological ecology, environmental impact factors

Nutrients

The canonical Redfield (1934) stoichiometric ratio (atomic ratio of carbon (C), nitrogen (N), and phosphorus (P)) in algae across the pelagic parts of the world ocean was established at 106:16:1. Using more recent data (1970–2010) this was slightly corrected to 163:22:1 (Martiny et al. 2014). Presently, the Redfield and Martiny et al. ratio is considered as a general average rather than a strict prerequisite for marine algae growth.

With regard to *E. huxleyi*, there were multiple reports that phosphorus limitation is critically important for the development of a bloom because of both an exceptionally high affinity of this alga to orthophosphate (Riegman et al. 2000; Paasche 2002) and its mixotrophic capability (Godrijan et al. 2020). *E. huxleyi* blooms do form exclusively if NO_3:PO_4 is >16, and reach their maximum at NO_3:PO_4 >25. Nevertheless, particularly high NO_3:PO_4 ratios are not indispensable for the occurrence of the massive development of this alga, as can be seen in the Barents Sea. Moreover, there are many reports of *E. huxleyi* blooms when NO_3:PO_4 was much lower than 16 (Mikaelyan et al. 2015; Silkin 2017). This might be explained by the mixotrophy of *E. huxleyi* if other sources were available for nutrition, such as organic nitrogen and phosphorus compounds. It explains the competitiveness of *E. huxleyi* in nutrient-depleted waters with regard to other co-occurring/competing algae. It is also shown that under N-depleted conditions, *E. huxleyi* susceptibility to photoactivation of photosystem (PS) II lessens (Loebl et al. 2010), which implies the ability of this alga to maintain PSII repair under high-light conditions typical of stratified surface waters.

It was shown that a phosphorus limitation does not enhance calcification (Oviedo et al. 2014), although it leads (strain specifically) to morphological changes in coccoliths and an increase in cell diameter. In phosphorus replete waters the growth rate increases, and cells and coccoliths become smaller. Conversely, a nitrogen limitation results in cell diameter decrease (Müller et al. 2008). Reportedly, phosphorus (but not nitrogen) starvation reduces the photosynthetic function of *E. huxleyi* (Silkin 2017). Unlike in N-depleted conditions, P-limitation leads to a decline in PSII functioning (Loebl et al. 2010).

The extended Redfield ratio also includes Fe as a micronutrient that can be limiting for the phytoplankton species. The ratio should be C:16 N:1 P:0.1 Fe:0.001. As part of cytochrome and ferrodoxin molecules, Fe is an important catalytic agent in the intracellular electron transport in enzymatic systems acting in photosynthesis and respiratory processes. It has been shown to be indispensable for the growth of large-celled phytoplankton (Martin et al. 1994), DNA repair and management of reactive oxygen species accumulation (Segovia et al. 2018) despite the ample availability of macronutrients. Conversely, small-celled *E. huxleyi* are much more tolerant to Fe-limitation (Miller et al. 1991), and in combination with selective grazing (only by specific zooplankton), *E. huxleyi* is able to form uni-species blooms as it is invariably observed, e.g., in the Gulf of Alaska (Moore et al. 2012), and in the part of the Pacific Ocean known as a «high-macronutrient-low-chlorophyll» area (Muggli and Harrison 1996).

Acidification

This issue is of particular importance in light of ongoing climate change and associated enhancement of CO_2 fluxes into the ocean (Eq. 2).

As the physiological response of *E. huxleyi* to rising CO_2 is strain-specific (Lorenzo et al. 2019) and depends on other co-occurring abiotic and some biotic factors, the actual effect may be synergistic, antagonistic, or even neutral (Boyd and Hutchins 2012). Moreover, the net effect might be short-term and long-term specific (Schlüter et al. 2014). This can explain the variable and seemingly contradictory results.

There are multiple lines of evidence that ocean acidification (elevated pCO_2/reduced pH) exerts a negative effect on calcification and the cellular PIC:POC ratio in *E. huxleyi*, and it is not consequential for photosynthesis (Meyer and Riebesell 2015). At the same time some strains showed an optimum curve in response to increasing pCO_2 (Bach et al. 2011; Sett et al. 2014), no significant response (Richier et al. 2010) or increased calcification rates (Iglesias-Rodriguez et al. 2008; Fiorini et al. 2011).

Reports on photosynthesis response vary between no response (Richier et al. 2010; Fiorini et al. 2011), increase (Rokitta and Rost 2012), decrease in photosynthesis rates (Bach et al. 2011; Shi et al. 2009), and variation with an optimum curve was obtained (Gao et al. 2009). The PIC/POC ratios are reported as generally decreasing with increasing pCO_2 (Bach et al. 2011; Rokitta and Rost 2012; Shi et al. 2009; Feng et al. 2018), although some works either have not found any change (Richier et al. 2010) or observed an increase (Fiorini et al. 2011). At least in the tropical ocean, coccolithophore calcification may not be decreasing with the ongoing acidification in oligotrophic waters (Maranon et al. 2016). As according to the Maranon et al. observations, the calcification: primary production ratio did not decrease with decreasing $[HCO^-_3]/[H^+]$ (Eq. 1-2), this might be a strong indication that carbonate chemistry is not consequential with regard to calcification at the community level throughout the tropical ocean pelagic zone. In nutrient replete marine environments, CO_2 elevation may hinder *E. huxleyi* growth (Hayden 2013), but can also encourage growth (Rivero-Calle et al. 2015). Similar reports come from latitudinally varied marine environments (e.g., Scottish coastal waters (León et al. 2018)). Young et al. (2014) generalize this assertion stating that, on balance, the impact of ocean acidification is «likely low, variable between strains, and reduced by adaptation and strain selection». Bach et al. (2013) found that *E. huxleyi* growth and photosynthesis rates were sensitive to low rather than high CO_2. Comparing the concomitant influence of atmospheric CO_2 increase, water temperature, salinity, irradiance, the latter three might be even more consequential (Sett et al. 2014; Charalampopoulou et al. 2016; Feng et al. 2018). At least, water temperature strongly modulates optimum growth and calcification rates (Sett et al. 2014). However, ocean acidification might promote carbon fixation as organic matter by calcifying *E. huxleyi* (Lorenzo et al. 2019). Water temperature and irradiance rather than pCO_2 elevation are believed to be the main drivers of the observed poleward expansion of *E. huxleyi* (Winter et al. 2014), at least according to data from the Southern Ocean (Charalampopoulou et al. 2016; Smith et al. 2017; Feng et al. 2018). However, there might be other drivers, such as intensified ocean currents (Oziel et al. 2020) evoking putative changes in the foodwebs and biogechemical cycles.

Addressing *E. huxleyi* adaptation to elevated pCO_2 in water, Lohbeck et al. (2012) showed for asexual populations that the ensuing significantly higher calcification rates did not reoccur. It implies the possibility of adaptive evolution in coccolithophores, and hence the risk aversion of the whole ecosystem.

Bach et al. (2015) conjected that if *E. huxleyi* (as well as all coccolithophores) are unable to efficiently adapt to the projected increase in H^+, the calcification rate can be impeded unless this process is counteracted by elevation of oceanic HCO^-_3 due to enhanced dissolution of sedimented $CaCO_3$. But both processes are expected to take place over the forthcoming hundred thousand years: by that time the carbonate chemistry conditions might become steadily fitting for calcification. At least presently, it has been conjected based on the data from the Great Calcite Belt, that *E. huxleyi* cells, regardless of their large population sizes, may be near the limit of this species' capacity to adapt to ongoing ocean acidification (Smith et al. 2017).

Reportedly, nitrogen depletion affects *E. huxleyi* cell morphometry (size, volume, PIC production) more significantly than variations of aquatic CO_2 (Müller et al. 2012), and the sinking rate of N-limited cells seems lower than that of N-replete cells (Pantorno et al. 2013), which is essential in terms of bicarbonate pump functioning.

As in the real word, pCO_2 rise is inseparably linked with increased temperature, the collective impact of these two factors is expected to bring about a short-term decrease in cellular PIC:POC (Feng et al. 2009), and a long-term increase in this ratio (Schluter et al. 2014). This suggests that on a short-time scale (even within a few hours (Ramos et al. 2010)), this alga is able to rapidly acclimate its metabolic processes in response to changes in water acidity. After five years, the growth rates completely recovered at the upper thermal tolerance limit (~27°) and atmospheric $pCO_2 = \sim 1000$ µatm (as expected at the end of the present century). Assessing in the laboratory the sensitivity of *E. huxleyi* morphotypes to acidification, Müller et al. (2015) found that under future acidification scenarios the PIC:POC ratio would drop especially strongly in B/C rather than in A and A-over-calcified strains. It was also found that long-term exposure of *E. huxleyi* to elevated CO_2 (850 µatm) and temperature (~ 24°) increases calcification but not expression of the calcification-related genes (Benner et al. 2013).

However, it remains unclear whether the above results from monocultural experiments are equally valid for the natural environment where nutrient availability, stratification, light availability, and some other factors are also important. Some studies have already addressed the issue of interactive effects on *E. huxleyi* responses (Feng et al. 2018; Nissen et al. 2018; Stelmakh and Gorbunova 2019; Pozdnyakov et al. 2019). Nonetheless, in naturally acidified waters of the Eastern South Pacific (where pH <7.8) the *E. huxleyi* community was dominated by A-over-calcified morphometric strains (von Dassow et al. 2018).

Global climate change will affect the exposure of algae to ultraviolet and photosynthetically active radiation (PAR) through changes in stratospheric ozone concentration, cloud albedo, concentrations of dissolved organic matter, and temperature-induced surface ocean stratification. However, Lorenzo et al. (2019) found that pCO_2 elevation did not significantly affect the photosynthetic sensitivity of *E. huxleyi* cells to ultraviolet (280-400 nm) and PAR radiation (400-700 nm). This might be explained by less light absorptivity of *E. huxleyi* cells under elevated pCO_2. However, exposure above a certain threshold inhibit *E. huxleyi*, because the repair rate becomes insufficient. It is notable that the photosynthetic apparatus of *E. huxleyi* shows a remarkable plasticity/acclimation faculty: this alga is able to withstand both high light conditions but at very low irradiance levels: Balch et al. (2014) report on under-ice vegetation of this alga, although they do not form a monospecific bloom in these conditions.

Environmental factors conditioning *E. huxleyi* blooms

Numerous studies found that water temperature, salinity, alkalinity/acidity, water column stratification, water movements (wind-driven vertical forcing, currents, eddies, fronts, advection), nutrients and trace metals availability, viruses infection, microzooplankton grazing, cysts seeding, water surface illumination, wind and wave driven surface water mixing, large-scale atmospheric baric formations, and air mass transport/decadal oscillations could all act as forcing factors (FFs) capable of affecting *E. huxleyi* blooms seasonally and, more importantly, interannually (Riebesell et al. 2000; Paasche 2002; Thierstein and Young 2004; Lipsen et al. 2007; Tyrrell and Young 2009; Rivero-Calle et al. 2015; Balch et al. 2016; Stelmakh and Gorbunova 2019). Against the background of longer-term changes in ocean acidification and water salinity, these factors may act both directly and through a sophisticated system of feedback mechanisms. It is therefore a challenge to disentangle the individual effects of FFs from each other. The effects of different FFs have mostly been studied individually, or for a limited number of co-acting FFs in laboratory/mesocosm conditions, as has been partly illustrated in the above section. This largely explains the reported broad ranges of FFs within which the growth of *E. huxleyi* was possible or was enhanced, potentially leading to plume formation. Very often water temperature, salinity, and CO_2 are considered as the main FFs determining the growth and extent of *E. huxleyi* blooms. Although valuable per se, such studies on a very limited number of environmental variables could not simulate the resulting impact of the entire set of FFs concomitantly acting under realistic conditions.

Notwithstanding the remarkable ability of *E. huxleyi* to grow under conditions unfavorable for algae of other taxonomic and functional groups (e.g., diatoms, flagellates, cyanobacteria), a highly irregular pattern of the registered two-decadal time-series of salinity, PIC, and ΔpCO_2 are indicative of a strong susceptibility of this alga outbursts to environmental forcing conditions (Kondrik et al. 2019; Silkin et al. 2019). Pozdnyakov et al. (2019) prioritized the FFs retrievable from two-decades of satellite data (1998–2019) from Subarctic and Arctic marine environments, viz. sea surface temperature and salinity (SST & Sal), PAR, water surface geostrophic current speed, mixed layer depth, and concentration of phytoplankton chlorophyll. Although the tested set of FFs did not explicitly include nutrient concentrations (NCs), the authors assumed that variations in the above variables indirectly account for the variations in NCs as well via such carbonate chemistry system parameters as alkalinity and basicity (Durairaj et al. 2015; Pozdnyakov et al. 2019). The representativeness of the employed FFs is supported by the fact that over the twenty years of observations the selected FFs have not failed to explain the patterns of either the areal extent or PIC content in *E. huxleyi* blooms. As expected, the prioritization results proved to be not only sea- but also time-specific: e.g., in the Barents Sea, SST was the most important FF, followed by PAR, while in the Bering Sea the sea surface salinity was the most important FF in the period 2001–2018, with PAR as a runner up, whereas SST was only in third place.

Although *E. huxleyi* is not generally considered to be a desired prey for zooplankton, nevertheless, some zooplankters can affect *E. huxleyi* blooms. In the Black Sea, up to 100% of the *Noctiluca scintillans* and *Oikopleura dioica* daily ration is constituted by *E. huxleyi* (Amelina et al. 2017). In the Barents Sea, large copepods *Metridia longa* and, to a lesser degree, *Calanus finmarchicus* are also reported as active consumers of *E. huxleyi* cells, however, their impact on the blooms was not directly assessed (Sergeeva et al. 2019). These findings fully support many of the earlier results from laboratory studies on *E. huxleyi* mortality due to grazing by copepods, including some of the earliest studies dating back to the early 1990s (Harris 1994).

Intra-annual and multi-year variations of *E. huxleyi* blooms in the current epoch of global warming

Rivero-Calle et al. (2015) conducted Random Forest statistical analysis of the in situ data from the Continuous Plankton Recorder Program executed in the North Atlantic during the last 45 years (1965–2010). They found that the occurrence of coccolithophore abundances over this time increased by more than 20%, while regional abundances in the 2000s proved to be at least ten times higher than in the 1960s. This long-term tendency was attributed to steadily increasing CO_2 and water temperature. Interannually, the observed variability was found to be modulated by the Atlantic Multidecadal Oscillation (AMO) through changes in the upward transport of nutrients, so that rising CO_2 and temperature and AMO (during positive periods) act conjointly. Nevertheless, these authors conjected that the observed growth rates might stabilize when pCO_2 reaches 500 ppm, i.e., in the really close future.

The time-series (January 2003-December 2010) obtained from satellite data (SCanning Imaging Absorption spectroMeter for Atmospheric ChartographY – SCIAMACY) for three regions in the world ocean (North Atlantic: at 53-63^{0}N, South Atlantic/eastern part of the Patagonian Shelf and South Pacific: at 38-48^{0}S) have not revealed any distinct tendency over that 8-year period, but there are appreciable interannual variations (Sadeghi et al. 2012).

Quantitative assessments of coccolithophore bloom areas (S) determined from Nimbus 7 CZCS imagery in the Subarctic North Atlantic (40-70^{0}N) and Subantarctic-Northern Antarctic (40-70^{0}S) latitudinal belts showed different patterns during 1979–1985. Whereas in the first region the bloom area declined, there was no evident trend in the second region. Extraordinarily high peaks in S were identified in 1980, 1983/1984, and 1985/1986 in the two regions, respectively (Brown and Yoder 1994).

Analyses of collated *in situ* databases from the Atlantic, Pacific, Indian, Arctic, and Southern oceans for the period 1991–2015 fail to show any clear patterns in $CaCO_3$ production (CP) distribution across the world ocean.

However, a strong relationship was established between cell abundance and CP, as well as CP surface and integrated CP (Daniels et al. 2018).

No significant tendencies in the areal coverage of coccolithophore blooms have been found from spaceborne images collected across 1997–2002 over the Black Sea, although there are large interannual variations. The Black Sea region is the second most important regarding the occurrence and extent of these algal (mostly *E. huxleyi*) blooms after the parts of the North Atlantic Ocean located above ~48^{0}N (Cokacar et al. 2004). Similarly, the surface distributions of *E. huxleyi* in the North Atlantic (35-68^{0}N) during 1998–2008 also shows large interannual variations, but no steady trend (Shutler et al. 2013). A similar result has been found from satellite observations of *E. huxleyi* blooms over Subarctic and Arctic seas for the period 1997–2013 (Kondrik et al. 2017): there was no indication of a sustained tendency in the occurrence of *E. huxleyi* blooms, but there were significant interannual variations both in the areal extent (S) (as exemplified in Fig.1 a-f) and CP. There is no tendency in variations of the integrated values of S in the time- series of blooms in either hemisphere over the period 1998–2010 (Moore et al. 2012). Kondrik et al. (2017) showed (Fig. 1) that blooms occurred annually in nearly 20 years of observations of subpolar and polar seas, but S and particulate inorganic carbon (PIC) varied between (<1 - 400) km^2 and (<1 to 250 kt) depending on the sea. Blooms within the Great Calcite Belt [~ (38-60), with the total area of 52·106 km] reportedly account for 26% of global PIC (Balch et al. 2016).

Despite the widespread lack of a tendency in bloom occurrence, *E. huxleyi* blooms in the central and especially northern parts of the Bay of Biscay displayed a distinct rise in bloom occurrence in the period 1979–2009 (Morozov et al. 2013). While there was no overall trend in *E. huxleyi* bloom occurrence in the Bering Sea, there was some interesting features of the interannual variability. There were two periods of remarkably massive blooms (in terms of both S and CP) during 1998–2001 and 2017–2019, and a significantly lower level of both S and CP in-between these periods of outbursts, which occurred in the wake of the strongest El Niño events during 1997–2019 (Lipsen et al. 2007; Pozdnyakov et al. 2020).

Intra-annual variations in S and PIC are bloom location-specific. Broadly speaking, *E. huxleyi* blooms develop in the wake of spring-time phytoplankton massive growth, which creates nutrient conditions favorable for *E. huxleyi* vegetation (Mikaelyan et al. 2015). Nonetheless, although the timing of bloom onset varies from year to year, *E. huxleyi* blooms are often reported to occur twice a year (as has been observed annually in the Black Sea since 1983 (Moncheva and Krastev 1997; Cokacar et al. 2004) or even for nearly the entire year (e.g., in the Bering Sea during 1997–2001; Kondrik et al. 2017, see Fig. 1f). Possibly they are stimulated by autumn noncalcifying phytoplankton blooming caused by intense entrainment of nutrients from below the euphotic zone (e.g., in the Black Sea), but in some other cases the respective driving mechanisms remain the subject of controversy and debate.

During the last decades, intra-annual variations in S, PIC, and the timings of bloom onset and duration are generally very significant as it is reported from a variety of marine environments, e.g., the Barents Sea (Smyth et al. 2004; Burenkov et al. 2011; Kondrik et al. 2017), Black Sea (Kopelevich et al. 2013; Mikaelyan et al. 2015; Kubryakov et al. 2019), Bay of Biscay (Morozov et al. 2013), North Atlantic (Shutler et al. 2013), Arctic Ocean (Petrenko et al. 2013), and world-wide (Brown and Yoder 1994; Moore et al. 2012; Sadeghi et al. 2012).

Future tendencies in *E. huxleyi* bloom dynamics in the warming climate

E. huxleyi have a remarkable physiological plasticity because the pan-genome allows associated transcriptional responses which assures the success of this alga in a variety of environmental conditions including those arising from nutrient limitations (Alexander et al. 2020) or acidification. However, these abilities do not imply a complete immunity of this alga to environmental changes including those resulting from ongoing climate change.

Expectedly, an increase in $_pCO_2$ is beneficial for *E. huxleyi* photosynthesis (and hence PIC production) rather than calcification as this alga has a relatively inefficient carbon concentrating mechanism. The latter responds positively to increases in HCO^-_3, and suffers from inhibition by increasing H^+ ions (Section 3). Therefore, in the forthcoming changing climate, the carbonate chemistry system would experience both detrimental and stimulating effects (Rivero-Calle et al. 2015).

Laboratory studies simulating the forthcoming climatological shifts (enhancement of ocean acidification and warming) seem strongly indicative that through evolutionary change, *E. huxleyi* is better suited to temperature adaptation than to acidification. Under combined enhanced warming and acidification, PIC production rose by 191% compared to non-adapted controls (Shutler et al. 2013).

Indeed, there is experimental evidence that *E. huxleyi* is vulnerable to frequent thermal variations, especially at elevated water temperatures expected in the future at lower latitudes (Wang et al. 2019).

Individually, climate models have large uncertainties in projected changes of the identified abiotic FFs that drive changes in *E. huxleyi*. This necessitates efforts to constrain model ensemble uncertainty, e.g., through subsampling based on the model skill in simulating historical climate. According to the selected best model ensembles (Gnatiuk et al. 2020) for scenarios of greenhouse gas concentration trajectory – RCP4.5 and RCP8.5, the main projected FFs changes in the Arctic are increasing sea surface temperature, declining sea water salinity, and reduction of short-wave solar radiation. The trends of changes in wind and current speeds are not statistically significant (~6x10^{-4} ms^{-1}yr^{-1} & ~10^{-4} ms^{-1}yr^{-1}, respectively). Simulations with a generalized coccolithophore model utilizing the input data from the Community Earth System Model Large Ensemble indicate that a 2-3° ocean temperature rise over the 21st century will entail a globally-averaged 10% increase in these species' growth (Krumhardt et al. 2017). At high latitudes, this increase is expected to proceed concomitantly with enhanced calcification. A ubiquitous doubling of oceanic pCO_2 will potentially lead to a moderate cell growth and a 25% decline in the calcification rate. Induced by warming, strengthening of surface ocean stratification may incur calcification intensification and a 25% reduction in growth because of nutrient depletion. Although such projections do not account for changes in the light limitation, *E. huxleyi* strains and co-occurring community species, a concomitant action of the above FFs will arguably result in dwindling calcification and growth rate in the majority of low to mid latitudes (but not at high latitudes) at the end of the current century (Krumhardt et al. 2017).

CONCLUDING REMARKS

Analysis of the reviewed publications suggests that all major and basic aspects of the *E. huxleyi* cell composition

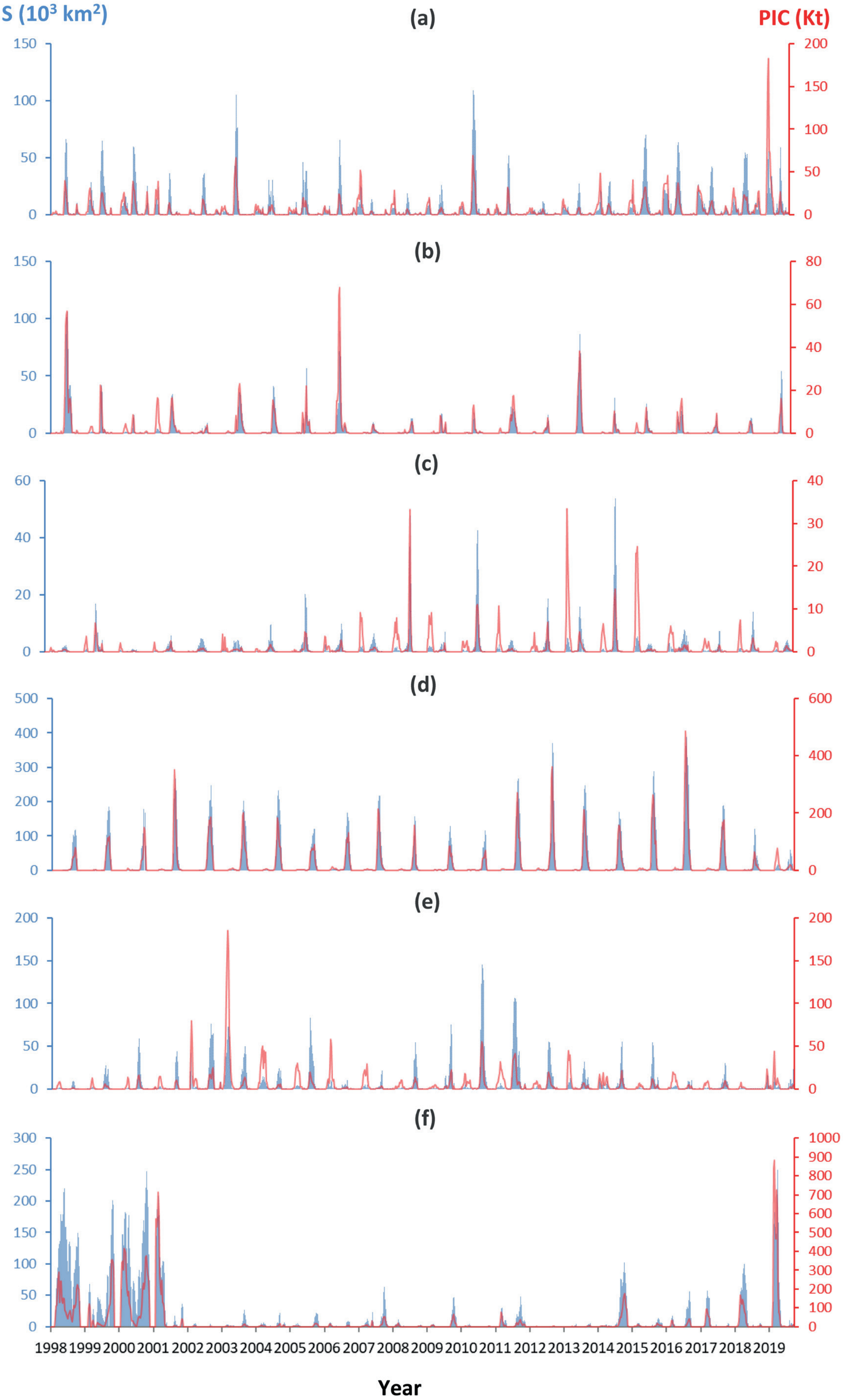

Fig. 1. Interannual variations in the occurrence of *E. huxleyi* bloom outbursts, their areal extent (blue line), and within-bloom PIC - particulate inorganic carbon content (red line) in the North (a), Norwegian (b), Greenland (c), Barents (d), and Bering (e) seas as retrieved from space observations during 1998–2019 (Kondrik et al. 2017, Pozdnyakov et al. 2020).

and functioning have been clarified to a large extent, and that indeed this alga is one of the best-studied marine organisms. At the same time, a wide range of important issues remain unexplored or insufficiently investigated. Not attempting to address all of them, we mention here only those that appear as serious obstacles to understanding and evaluating the present and future role of coccolithophores in the changing global environment.

In terms of cell morphology, there is still no insight into the causes and type of life cycle interchange between calcified diploid (2N) and non-calcified scale bearing haploid (1N) phases/forms (syngamy or meiosis?) or else between mutant naked diploid (2N) and haploid (1N) phases/forms (meiosis?). There is still no definitive prioritization of factors determining the formation and global geographic distribution of morphotypes A, B/C, overcalcified A and R forms.

With regard to genetic diversity, there is insufficient insight into how the core genome is complemented with specific genes conditioning the environmental fitness of *E. huxleyi* ecotypes to a wide range of environmental conditions, determining intricate intracellular transport routes (especially for Ca^{2+} ions), and initiation of the calcification reaction. The capacity of *E. huxleyi* to mixotrophy remains mostly conjecture, but is nevertheless a central issue in this alga nutrition depletion tolerance.

The physiological role of DMSP (as DMS precursor) in *E. huxleyi* cells and the driving factors/agents/mechanisms triggering DMSP breakdown reactions still remain obscure. Also, the organic and inorganic precursors of CH_4 produced in this alga are not sufficiently studied, particularly in conditions of calcium carbonate oversaturated waters.

A big issue is the environmental FFs affecting the formation of massive *E. huxleyi* blooms. Many FFs have been proposed, but results of investigations conducted primarily in laboratory/mesocosm conditions are of limited value because it is unclear how well they can translate to real conditions, particularly in terms of the variety of co-acting FFs. Meanwhile, the prioritization of FFs that can co-occur in real ocean conditions is of particular importance.

It is clear that due to the large extent and high intra- and interannual temporal variability of *E. huxleyi* blooms, use of satellite observations is the only means to perform statistically reliable FFs prioritization, quantification of bloom extent, release of calcite, enrichment of surface water with dissolved carbon dioxide, and trace down over long time periods the tendencies in the development of the *E. huxleyi* phenomenon and its environmental impacts. Such studies have already been conducted in individual seas, but they need to be extended to cover the entire world ocean.

Finally, in conjunction with the emerging global and regional climate models, biological models of *E. huxleyi* blooms applicable to the great variety of marine/oceanic environments are indispensable for forecasting (at least over a mid-term time-period) the forthcoming climatic and environmental role of *E. huxleyi* blooms in changing the world around us. Although the first tentative steps in this direction have been taken, much more effort is needed to develop and apply these models. ■

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