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Multifaceted Contributions of Coccolithophores to Ocean Carbon Export

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Coccolithophores, a type of unicellular calcifying algae, are widely distributed across the global ocean. They contribute to the ocean carbon cycle by producing organic and inorganic carbon. Hence, they function as multifaceted contributors to oceanic carbon pumps, the biological carbon pump (BCP) and the carbonate counter pump (CCP). Global climate change profoundly impacts ocean environments, leading to ocean acidification, increased sea surface temperature, and nutrient depletion, all of which influence the physiology of coccolithophores. The accumulation and subsequent sinking of carbon produced by coccolithophores contribute to the total carbon export in the water column. This article reviews the physiology and distribution of coccolithophores, expounds on the intricate contribution of coccolithophores to BCP and CCP separately, and summarizes how climate-induced alterations in environmental factors (e.g., temperature, nutrient supply, light, and carbonate chemistry) affect the carbon accumulation and sinking rate of coccolithophores on the basis of culture experiments and field investigations. This study provides a foundation for assessing the contribution of coccolithophores to carbon export under potential future global warming scenarios.

Introduction

Coccolithophores are a type of marine unicellular calcifying nannoplanktons that belong to the phylum Haptista [1,2] and class Prymnesiophyceae [3]. A coccolithophore cell is surrounded by orderly arranged calcite scales called coccoliths. Coccolithophores are widely distributed across the global oceans, commonly forming large-scale blooms at high latitudes, and are a dominant part of the global carbon biogeochemical cycle. Coccolithophores can produce both organic and inorganic carbon, serving as producers for both marine biological carbon pumps (BCPs) and carbonate counter pumps (CCPs) [4]. Field investigations have shown that coccolithophores can account for ~20% of total carbon fixation in unproductive central subtropical gyres [5] and almost all calcium carbonate production during a bloom in the Southern Ocean [6,7].

Global climate change has substantially altered the physical and chemical properties of seawater, exerting strong influences on coccolithophore physiology and ecology. For example, ocean acidification (OA) and warming have changed coccolithophore communities and their cellular organic and inorganic carbon production. Such a change in coccolithophores may greatly impact global ocean carbon cycling, which is an important issue to be considered by the scientific community. To this end, the present paper reviewed the characteristics of coccolithophore-based marine carbon pumps (i.e., BCP and CCP), as well as the responses of coccolithophores to OA, ocean warming, and nutrient depletion of the surface ocean, which could occur in future climate change scenarios.

Overview of Coccolithophores

Coccolithophores exhibit various morphological features and sizes, with cell sizes typically ranging from 3 to 40 μm [8]. The test formed by coccoliths (known as coccosphere) may be cylindrical, ellipsoidal, fusiform, obpyriform, ovoid, or spherical [9]. Coccoliths are produced intercellularly in the Golgi apparatus [10], serving as an important basis for taxonomy. The size of coccoliths commonly ranges from 0.5 to 20 μm [9,11]. Although coccoliths come in various shapes and architectures in plan view, they can be morphologically categorized into 3 main types in vertical cross-section: Murolith, Placolith, and Planolith [9]. Most coccolithophores exhibit haplo-diplontic life cycles, with the haploid stage of the coccolithophore producing holococcoliths or nannoliths and the diploid stage producing heterococcoliths. In the transitional state between 2 life-cycle phases, a coccolithophore-bearing combination coccosphere can be observed [12,13].

Some coccolithophore species have been extensively studied in culturing, with their cellular physiological processes comprehensively understood, serving as "model species". For example, *Emiliania huxleyi* is widely distributed in global oceans as

a cosmopolitan species, usually forming blooms that can be detected by satellite [14,15]. *Gephyrocapsa oceanica*, another type of "model species" common at midlatitudes and coastal regions [16], is slightly larger and more heavily calcified than *E. huxleyi* [12,17]. By 2005, over 280 coccolithophore species had been identified in modern oceans [11,12]. Coccolithophores prefer physicochemical conditions characterized by relatively high nitrate, low phosphate, and sufficient light availability [18,19]. Satellite remote sensing data from 1997 to 2010 indicate that coccolithophores frequently formed blooms [15], such as those documented in the Bering Strait [20,21], the North Atlantic [15,22–24], the Black Sea [25,26], and the Southern Ocean [15,27]. From 1979 to 1985, the global annual average area of coccolithophore blooms was estimated at 1.4×10^6 km^2, with over two-thirds occurring in high-latitude waters [27]. Using a threshold abundance of 1×10^6 cells/l for defining coccolithophore blooms [18,26,28], we identified more than 30 bloom events that were synchronically confirmed by field investigation and sampling. The global occurrences of coccolithophore blooms have been reviewed from 1955 to 2017 (Fig. 1 and Table 1). *E. huxleyi* was the most commonly bloom-forming species, followed by *G. oceanica*, and other species include *Pleurochrysis pseudoroscoffensis*, *Syracosphaera halldalii*, and *Umbellosphaera irregularis*. *E. huxleyi* blooms commonly occur on the east coast of the North Atlantic. Berge [29] recorded a cell abundance of 1.2×10^8 cells/l in 1955. In comparison, a *G. oceanica* bloom was found with a cell abundance of 1.8×10^7 cells/l in Jervis Bay in 1992 [30]. *E. huxleyi* and *G. oceanica* are common coccolithophores in the Chinese seas (the East and South China Seas); however, almost no such blooming events have been recorded [31,32].

Ecological Effects of Coccolithophores on the Marine Carbon Cycle

The ocean, as a large carbon reservoir, plays an indispensably pivotal role in the global carbon cycle. Between the early 1960s and the late 2010s, the oceans have absorbed about 25% ± 2% of anthropogenic CO_2 emissions, with an average sinking rate of 2.7 ± 0.3 pg C per year [33]. The process that transfers carbon to the deep sea is known as carbon export. The processes that facilitate oceanic carbon absorption include the solubility pump, CCP, BCP, and microbial carbon pump (MCP) [34,35]. Importantly, coccolithophores contribute to both BCP and CCP as an essential component of the marine carbon cycle given their considerable biomass.

BCP and CCP

BCP denotes the process where phytoplankton photosynthesis converts dissolved inorganic carbon (DIC) into particulate organic carbon (POC) (Eq. 1), which is subsequently exported to the deep sea via processes such as self-sedimentation and food webs [36–38].

$$CO_2 + H_2O \leftrightarrow (CH_2O) + O_2 \quad (1)$$

Coccolithophores and other autotrophic marine planktons absorb seawater aqueous CO_2 through photosynthesis, converting

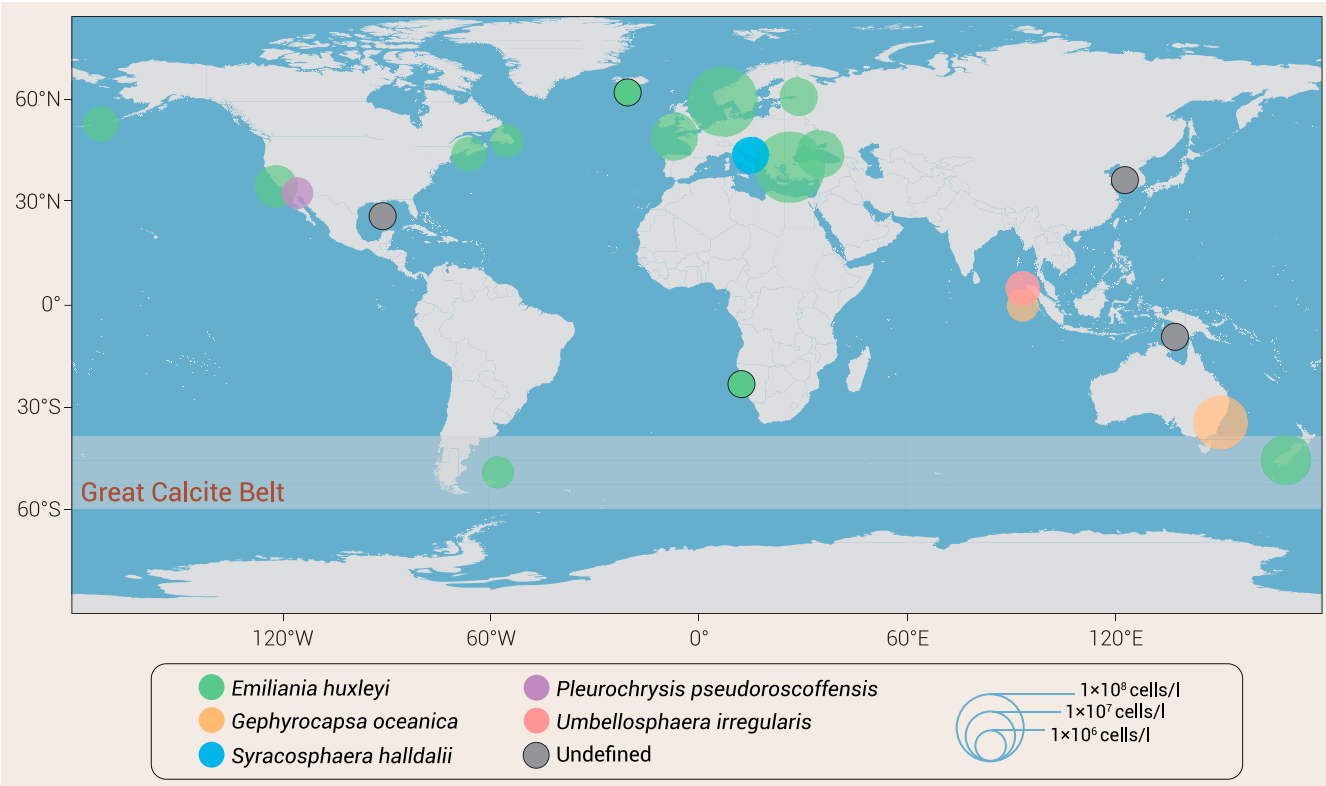

Fig. 1. Global distribution and cell abundance of coccolithophore blooms between 1955 and 2017. In the case of multiple records in a region, only the record with the highest abundance is labeled. Opaque circles with a black stroke indicate that no cell abundance data are available.

Table 1. Records of coccolithophore blooms from 1955 to 2017. Bold texts indicate satellite-based observations.

Sampling period	Area	Dominant species	Bloom area (km^2)	Abundance (cells/l)	Reference
July 1955	Western Norway	*E. huxleyi*	—	1.2×10^8	Berge [29]
November 1977	Eastern Bering Sea Shelf	*E. huxleyi*	2.0×10^5	$2.1–2.8 \times 10^6$	Sukhanova and Flint [20]
1979	Western North Atlantic Ocean	*E. huxleyi*	4.4×10^5	—	Brown and Yorder [23]
1980	Western North Atlantic Ocean	*E. huxleyi*	8.1×10^5	—	Brown and Yorder [23]
1981	Western North Atlantic Ocean	*E. huxleyi*	1.6×10^5	—	Brown and Yorder [23]
1982	Western North Atlantic Ocean	*E. huxleyi*	4.6×10^5	—	Brown and Yorder [23]
May 1982	Northeast Atlantic	*E. huxleyi*	—	8.5×10^6	Holligan et al. [14]
1983	Western North Atlantic Ocean	*E. huxleyi*	1.7×10^5	—	Brown and Yorder [23]
1984	Western North Atlantic Ocean	*E. huxleyi*	2.0×10^4	—	Brown and Yorder [23]
1979–1985	Yellow Sea	—	$7.3 \pm 10.7 \times 10^4$	—	Brown and Yorder [27]
1979–1985	Arafura Sea and Gulf of Carpentaria	—	$1.1 \pm 0.89 \times 10^6$	—	Brown and Yorder [27]
1979–1985	Gulf of Mexico	—	$2.3 \pm 1.1 \times 10^5$	—	Brown and Yorder [27]
1985	Western North Atlantic Ocean	*E. huxleyi*	5.1×10^4	—	Brown and Yorder [23]
July 1988	Gulf of Maine	*E. huxleyi*	5.0×10^4	1.8×10^6	Balch et al. [158]
June 1989	Gulf of Maine	*E. huxleyi*	5.0×10^4	1.6×10^6	Balch et al. [158]
June 1991	Northeast Atlantic	*E. huxleyi*	2.5×10^5	—	Fernández et al. [22]
August 1991	Nova Scotian Shelf and Grand Bank	*E. huxleyi*	—	1.5×10^6	Brown and Yorder [159]
May 1992	Western Norway	*E. huxleyi*	—	7.0×10^6	Kristiansen et al. [160]
June 1992	Western English Channel	*E. huxleyi*	—	2.0×10^6	Garcia-Soto et al. [161]
November 1992	Big Glory Bay	*E. huxleyi*	—	9.6×10^6	Rhodes et al. [162]
December 1992	Jervis Bay	*G. oceanica*	—	1.8×10^7	Blackburn and Cresswell [30]
June 1993	Northern North Sea	*E. huxleyi*	—	3.5×10^6	Buitenhuis et al. [163]
July 1993	North Sea	*E. huxleyi*	—	1.2×10^6	van der Wal et al. [164]
June 1994	Northern North Sea	*E. huxleyi*	—	4.5×10^6	Head et al. [165]
April 1998	Bay of Biscay	*E. huxleyi*		3.2×10^6	Lampert et al. [28]
June 1999	North Sea	*E. huxleyi*	—	1.5×10^6	Rees et al. [166]
June 1999	Salton Sea (California)	*P. pseudoroscoffensis*	—	1.0×10^6	Reifel et al. [167]
June 1999	Northern North Sea	*E. huxleyi*	2.0×10^3	2.3×10^6	Widdicombe et al. [168]
February 2000	Equatorial Indian Ocean	*U. irregularis*	—	1.4×10^6	Guptha et al. [169]

(Continued)

Table 1. (Continued)

Sampling period	Area	Dominant species	Bloom area (km^2)	Abundance (cells/l)	Reference
February 2000	Equatorial Indian Ocean	*G. oceanica*		1.0×10^6	Guptha et al. [169]
May 2002	Black Sea	*E. huxleyi*		3.8×10^6	Mikaelyan et al. [26]
May 2002	Northeast Atlantic	—	—	3.9×10^6	Moore et al. [15]
March/April 2003	Namibian coast	*E. huxleyi*	—	—	Siegel et al. [170]
June 2004	Northern Bay of Biscay	*E. huxleyi*	—	8.0×10^6	Harlay et al. [171]
June 2004	Black Sea	*E. huxleyi*	—	8.2×10^6	Mikaelyan et al. [26]
June 2005	Black Sea	*E. huxleyi*	—	2.7×10^6	Mikaelyan et al. [26]
May 2006	Black Sea	*E. huxleyi*	—	4.4×10^6	Mikaelyan et al. [26]
June 2007	Black Sea	*E. huxleyi*	—	1.3×10^6	Mikaelyan et al. [26]
December 2008	Patagonian Shelf	*E. huxleyi*	—	1.0×10^6	Balch et al. [172]
June 2012	Black Sea	—	—	1.6×10^7	Kubryakov et al. [25]
June/July 2012	North Atlantic	*E. huxleyi*	—	3.3×10^6	Sheyn et al. [24]
June 2015	Santa Barbara Channel	*E. huxleyi*	1.2×10^3	5.7×10^6	Matson et al. [173]
June 2017	Black Sea	—	—	2×10^7	Kubryakov et al. [25]
October 2017	Mediterranean Sea	*S. halldalii*	—	2.3×10^6	Skejić et al. [174]

DIC into POC, which is mostly used in the euphotic zone. With seasonal variations, approximately 1%–40% of net primary productivity is transported below the euphotic zone through the BCP [39]. Ultimately, only 0.3% of the POC produced in the surface ocean is buried in seafloor sediments [40]. BCP plays an instrumental role in the process of oceanic sequestration of atmospheric CO_2. Furthermore, active dissolved organic carbon, associated with coccolithophores or food webs, can be transformed into recalcitrant dissolved organic carbon (RDOC) through MCP, which is resistant to degradation and serves as a more stable organic carbon reservoir [41].

CCP refers to the process by which marine calcifying organisms (e.g., foraminifera, pteropods, and coccolithophores) synthesize calcium carbonate shells (also known as particulate inorganic carbon [PIC]) from calcium and bicarbonate ions. PIC is then precipitated in the water column, where it partially dissolves and is partially buried in marine sediments. The term "counter" actually reveals that the biological production of $CaCO_3$ coincides with the release of CO_2 (Eq. 2) [42].

$$Ca^{2+} + 2HCO_3^- \leftrightarrow CaCO_3 \downarrow + CO_2 \uparrow + H_2O \quad (2)$$

The theoretical formula posits that producing one unit of $CaCO_3$ requires the release of one unit of CO_2, whereas field observation data indicate that the actual ratio of CO_2 gas to precipitated $CaCO_3$ is 0.6 (Ψ) in surface seawater at 25 °C. Therefore, an improved equation (Eq. 3) has been proposed [43]:

$$\begin{aligned} Ca^{2+} + 2HCO_3^- \leftrightarrow CaCO_3 \downarrow + \Psi\left(CO_2 \uparrow + H_2O\right) \\ + (1-\Psi)\left(CH_2O + O_2\right) \end{aligned} \quad (3)$$

$$\Psi = CO_2 \uparrow / CaCO_3 \downarrow$$

The overall equation indicates that despite CO_2 being emitted from the reaction, not all carbon atoms return to the atmosphere. Instead, because of the buffering of the seawater carbonate system, a portion of the released CO_2 is reconverted to HCO_3^-.

In addition to the functions of BCP and CCP, coccolithophores also consume dissolved organic matter (DOM) as a carbon source. Coccolithophores are often recognized as photoautotrophs, but heterotrophic types (e.g., osmotrophic) are also found in coccolithophores. For example, *Syracosphaera* spp. can use lactate as a carbon source [44]. In this regard, Thomsen et al. [45] found that some coccolithophores in polar water are plastidial heterotrophic. DOC absorbed by coccolithophores through osmotrophy can be further transformed into both PIC and POC. Heterotrophic or osmotrophic ecology is a strategy in low-light conditions, such as in the lower euphotic zones; more importantly, the captured DOC becomes a part of particulate carbon, accelerating their sinking velocity (or increasing carbon cycling) [46]. It also represents an easily overlooked part of the coccolithophores' contribution to the ocean carbon biogeochemical cycle. However, the quantities of carbon that originate in the DOM via coccolithophore assimilation must be further investigated.

CCP is instrumental in preserving the disparities in the vertical gradient of oceanic DIC and total alkalinity. PIC precipitation, which consumes bicarbonate in the ocean's surface layer, reduces the DIC and total alkalinity in the ocean's upper layers. The calcium carbonate produced redissolves into bicarbonate ions under low temperatures and high pressures in the deep

sea, thereby releasing DIC and total alkalinity in deeper seawater layers. Meanwhile, BCP can synergize with CCP to promote oceanic carbon storage; that is, during gravitational settling, PIC can encapsulate and carry POC (including POC produced by noncalcareous organisms) because of its high density and sinking rate, thus accelerating the export of POC and protecting POC from remineralization through the ballast effect [47]. The White Cliffs of Dover (UK) is a landscape formed by carbonate precipitation and fossilization caused by coccolithophore blooms [48]. In marine anoxic sediment environments, microorganisms such as denitrifying bacteria can increase the HCO_3^- alkalinity of the interstitial water. Conversely, RDOC can become a carbonate crystal nucleus, and the resulting coupling of MCP with CCP can increase microbial-driven carbonate precipitation, which adds to inorganic carbon storage in marine sediments [41].

Contribution of coccolithophores to marine carbon export

As depicted in Fig. 2, coccolithophores convert DIC to POC via photosynthesis, whereas PIC is produced and precipitated through calcification. Because of their considerable biomass (Table 1), coccolithophores contribute substantially to the global ocean's POC export, and they have long been acknowledged as a major contributor to the export of marine calcium carbonate to the deep sea [6,7]. In the Southern Ocean waters, PIC derived from coccolithophore blooms constitutes a crucial part of calcium carbonate production and its deep-sea export. Notably, the sinking flux of calcium carbonate from *E. huxleyi* accounted for 85% of the annual PIC export in this area from 2011 to 2012 [49]. In this respect, Sprengel et al. (2002) analyzed coccolithophore fluxes in waters off the Canary Islands in the North Atlantic in 1997. They discovered that in this region, coccolithophore calcium carbonate fluxes could be up to 2.8 g m^{-2} a^{-1}, representing 31%–33% of the annual carbonate flux [50]. Meanwhile, Jin et al. [51] found that *E. huxleyi* and *G. oceanica*, the most predominant coccolithophores, contributed ~18% to the surface PIC inventory in the South China Sea.

Within the euphotic zone, coccolithophores produce a high amount of particulate carbon. However, their impact on oceanic carbon sequestration is complex. One primary mechanism involves calcification, which reduces both ocean total alkalinity and DIC in upper seawater, thereby decreasing atmospheric CO_2 uptake by this ocean layer. Conversely, POC generated by coccolithophore photosynthesis is transported to deeper ocean layers, enhancing oceanic carbon sequestration [52]. Simultaneously, because of their density and slow dissolution rate, coccoliths can ballast POC sinking or other organic carbon forms (e.g., detritus and excreta) to the deep sea, thereby increasing the BCP efficiency [47]. Evidently, assessing coccolithophores' contribution to carbon export requires a comprehensive understanding of their cellular carbon production.

The physiology associated with coccolithophores' POC and PIC production serves as a crucial metric for assessing their contribution to ocean particulate carbon export. Carbons are

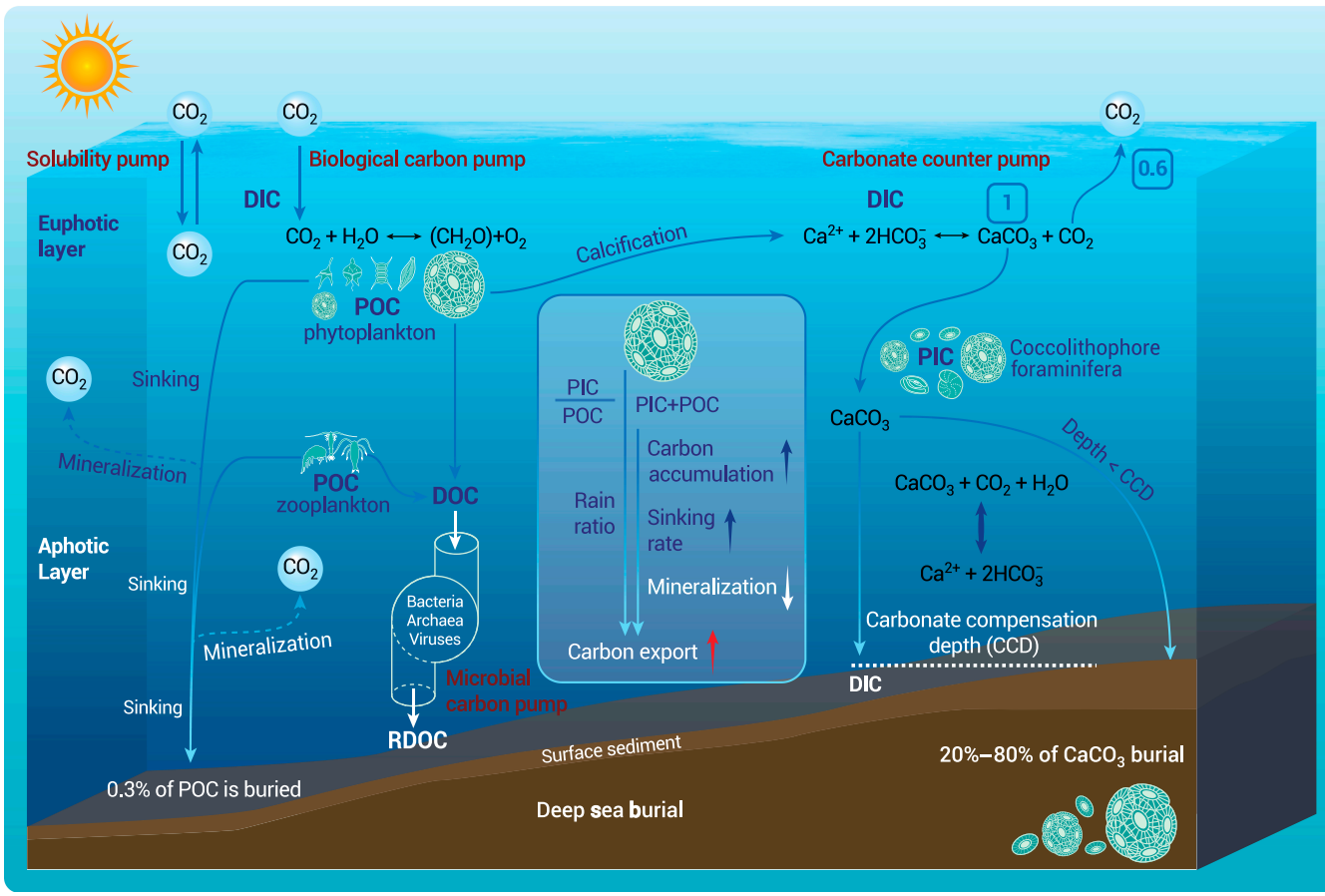

Fig. 2. Contribution of coccolithophores to marine carbon export.

transported to the deep sea via BCP and CCP, respectively, representing the "quantity" of carbon stored by the coccolithophore under ideal conditions. In practical experiments, the parameters measured for monitoring coccolithophore physiology consist of growth rate, PIC and POC quota per cell, and the PIC-to-POC ratio (PIC:POC). However, owing to bacterial remineralization and other factors, only ~0.3% of POC can sink to the seabed [40]. Therefore, the sinking rate must be considered. This parameter characterizes the efficiency of coccolithophores in exporting carbon [53]; higher sedimentation rates can mitigate POC attenuation due to remineralization. By combining particulate cellular carbon production with the sinking rate, we can quantify the contribution of coccolithophores to carbon export to a certain degree. Coccolithophore PIC:POC is an important parameter in the global carbon cycle [54], determining the relative strength of BCP versus CCP at the cellular level. When coccolithophore PIC:POC is lower than a critical value that depends on the ambient seawater carbon chemistry, the net effect of coccolithophore growth is a source of CO_2 and vice versa [55]. For example, such a threshold value can be 1.65 with a seawater pCO_2 of 360 μatm at 25 °C [56]. The PIC:POC of coccolithophores can vary from 0.1 to 3.0 due to species differences and environmental changes [17].

Potential Changes in Carbon Accumulation and Sinking Rate of Coccolithophores under Global Change

Since the Industrial Revolution, human activities have led to drastic changes in the physical and chemical properties of the ocean. The surge in carbon dioxide emissions due to fossil fuel combustion has directly resulted in OA, elevated surface water temperatures, and nutrient limitation. Various environmental factors greatly impact marine organisms and perpetually transform marine ecosystems. These diverse environmental factors account for the changes in coccolithophores, and coccolithophores respond in multiple aspects, encompassing regulatory effects on their photosynthesis and calcification. Based on culture experiments and field investigations, the impacts of OA, surface water warming, alterations in light intensity, and nutrient limitation on coccolithophore cellular carbon production are discussed, with *E. huxleyi* serving as a model species for illustration. Furthermore, a brief description of the combined effects of environmental factors is given. Although coccolithophores can exhibit species- or strain-specific responses to certain environmental changes, some general physiological features can be summarized.

Ocean acidification

Serving as an important atmospheric carbon "sink", the ocean is the fate of most anthropogenic CO_2 [57]. Since 1750, atmospheric CO_2 concentrations have increased by 47% and will continue to rise in the future [58]. The CO_2 absorbed by seawater has caused intensified OA, as suggested by a decrease in seawater pH and CO_3^{2-} concentration, an elevation in HCO_3^- concentration, and a shallowing in the carbonate compensation depth (CCD) [59,60]. If CO_2 emissions are not effectively curtailed, atmospheric CO_2 levels are expected to reach 950 ppm by the end of this century, with pH continuing to drop by 0.3 to 0.5 [61].

OA leads not only to a decrease in seawater pH but also to changes in the composition of seawater carbonate chemistry. The combined effects of these 2 processes on coccolithophore photosynthesis and calcification are dual-faceted. Because of the species and strain specificity of coccolithophores, along with variations in laboratory culture conditions, the responses of coccolithophore organic and inorganic carbon production to acidification have inconsistent results. For example, Iglesias-Rodriguez [62] experimentally demonstrated a significant increase in both PIC and POC contents of *E. huxleyi* NZEH with CO_2 increase from 490 to 750 ppmv, whereas the cellular PIC:POC ratio remained unchanged. Meanwhile, de Bodt's [63] study revealed a decrease in cellular PIC production and PIC:POC, with no significant change in POC production for *E. huxleyi* AC481 under OA conditions. In contrast, Bach et al.'s [64] results on *E. huxleyi* PMLB92/11A exhibited an optimal curve response for PIC production, characterized by a sharp increase from the lowest to 40-Pa CO_2, followed by a decline with increasing pCO_2 and a decreasing trend in PIC:POC. Overall, most studies found that acidification leads to reduced PIC productivity [65,66] and lower PIC:POC of coccolithophores [63,64,66,67].

Additionally, variations in the growth period of coccolithophores can also contribute to discrepancies in the experimental results. In the long-term acidification acclimation experiment of Jin and Gao [68], *G. oceanica*'s POC production from generations 670 to 1,564 under high CO_2 levels was 7.8% higher than that under low CO_2 partial pressure, whereas this difference became insignificant when culturing cells from generation 1,564 to 2,000. Schlüter et al. [69] discovered that the continuous cultivation of *E. huxleyi* for 2,100 generations in an acidified environment decreased PIC production. However, when the culture conditions were restored to normal levels, calcification remained consistent with the control, indicating the adaptive evolution of coccolithophores in response to OA.

Biermann and Engel investigated variations in the sinking rate of *E. huxleyi* aggregates under diverse CO_2 levels, revealing a roughly 3.5-fold decrease under high CO_2 conditions. Furthermore, they found that high CO_2 levels increased the formation of calcite aggregates and their bacterial content [70]. Similarly, Xi's study [71] showed a 39.6% reduction in the sinking rate of coccolithophores when the CO_2 concentration increased from 800 to 1,500 ppm.

From the perspective of ancient oceans, Beaufort et al. [72] discovered a long-term decrease in coccolith mass from the last glacial maximum (~20 kyr before the present) to the Holocene. This period coincides with an increase in atmospheric CO_2 concentration from 180 to 280 ppm [72,73]. Their results indicate that (a) individual coccoliths become less calcified in response to OA and (b) the decrease in coccolith mass results from a transition of the coccolithophore community from heavier to lighter coccoliths due to increased seawater CO_2.

Increased sea surface temperature

Temperature is a critical factor for phytoplankton growth, and phytoplankton growth rates reach their peak at optimal temperatures [74]. The phytoplankton response to temperature encompasses genotypic [75] and phenotypic variations [76,77]. Temperature influences the phytoplankton community, leading to modifications in community composition and succession [78]. Concurrently, a rise in surface seawater temperature inevitably intensifies seawater stratification, resulting in a decrease in nutrient supply from the deep sea to the surface layer [79,80].

Commonly, phytoplankton growth rates positively respond to temperature, but a continuous rise in temperature beyond

the optimal range for various coccolithophore species and strains can cause a decline in cellular growth rate [65,77,81–83]. Therefore, it can be predicted that with warming surface waters, coccolithophore species with low optimum temperatures would move toward the poles. Paleofossil evidence shows significant shifts in coccolithophore biogeography and abundance during the rapid warming event of the Paleocene–Eocene turnover (56 Ma). Coccolithophores vanished entirely at lower latitudes, restricting themselves to colder waters [84]. In addition, recent observations (from 1947 to 2009) indicated a poleward migration of *E. huxleyi* coccolithophore blooms [85–88].

Pooled analysis of data from species and strains of coccolithophores revealed that the highest value of PIC:POC commonly occurs when the temperature ranges from 15 °C to 20 °C [17,66,81,89]. The POC content of different strains of *E. huxleyi* was often observed to be insensitive [81,89] or decreasing [89,90] in response to warming, and similarly decreasing trends were observed for *Syracosphaera pulchra* [91] and *Coccolithus pelagicus* [92]. Coccolithophores tend to reveal a pronounced decrease in warming in PIC contents [81,89,90,92,93]. In terms of sinking rate, calcified strains of coccolithophores responded differently from noncalcified strains. The sinking rate of calcified strains decreased when the temperature was increased from 15 °C to 25 °C. However, the noncalcified strains reached a maximum sinking rate at 20 °C [71,81]. Genotype differences in various coccolithophores were one of the reasons why studies on the effect of temperature on photosynthesis and calcification in coccolithophores did not yield consistent results.

Ocean warming is associated with fluctuating temperature changes. Wang et al. [82] examined the physiological and ecological responses of *E. huxleyi* to warming and temperature variations, revealing a reduction in the growth and calcification rates of *E. huxleyi* due to these factors. Similarly, Wang et al. found that for *E. huxleyi* RCC1266, warming and temperature variations notably decreased the sinking rate. According to Stokes' law, cell density and size are the key determinants of the sinking rate. A decrease in cellular PIC content due to warming indirectly lowers cell density, reducing the sinking rate and diminishing the carbon export capacity of coccolithophores [81].

Light

Light serves as the primary energy source for phytoplankton growth. Coccolithophore blooms frequently occur in areas and seasons with high light intensity (≥25 μmol photons m^{-2} s^{-1}). Climate-change-induced alterations in light intensity affect coccolithophores in 2 ways. First, surface water warming intensifies seawater stratification, leading to increased light availability for phytoplanktons in the euphotic zone [94,95]. The augmentation of photosynthetically active radiation (PAR) boosts *E. huxleyi*'s photosynthetic rate or POC production [96–99]. However, fluctuating outdoor light (without UV radiation) decreases the growth rate of coccolithophores [100]. The effect of PAR on coccolithophore calcification has yielded varied conclusions among researchers (Table 2). Nimer and Merrett [99] and Zondervan et al. [101] found that *E. huxleyi*'s calcification rate was amplified with increased PAR. However, some researchers noted a decrease in PIC production [102,103] and PIC:POC values [66,102,103] when PAR was elevated from 50 to 400 μmol photons m^{-2} s^{-1}—a phenomenon that can be explained by the fact that the energy requirement for calcification in coccolithophores is only 19% of that for photosynthesis [104]. In contrast, Xi's research [71] indicated a significant increase in *E. huxleyi*'s PIC content and PIC:POC with an increase in light from 50 to 500 μmol photons m^{-2} s^{-1}, corresponding to an approximately 6-fold increase in *E. huxleyi*'s sinking rate.

Second, ozone layer depletion has increased the amount of medium-wave ultraviolet radiation (UVR, 280 to 400 nm) reaching Earth's surface, comprising UV-A (280 to 315 nm) and UV-B (315 to 400 nm). UVR (especially UV-B) tends to inhibit photosystem II [105], damages DNA molecules [106], and influences biological growth rates [107]. In this respect, coccoliths can serve as a protector for UVR resistance. Calcified coccolithophores can grow up to 3.5 times faster than noncalcified cells under UVR (twice as fast under indoor light) [108]. However, UVR irradiation in nature also significantly reduces calcified coccolithophore growth rates [100,108,109]. This may reflect *E. huxleyi*'s trade-off between growth rate and cellular self-repair under UVR, accompanied by the production of UV-absorbing compounds [100]. *E. huxleyi*'s calcification rate

Table 2. Summary of available research on diverse responses of coccolithophores to PAR. Symbols: ↑ represents positive effects; ↓ represents negative effects; → represents no significant effect; ∩ represents optimal response; / represents data loss; * indicates data calculated based on PIC and POC production rate and growth rate (μ) from the article in the following formulas: PIC production = (PIC/cell) × μ, POC production = (POC/cell) × μ.

Species/Strain	Light intensity (μmol photons m^{-2} s^{-1})	POC content	PIC content	PIC/POC	Reference
E. huxleyi PML B92/11	15–150	↑	↑	↑	Zondervan et al. [101]
E. huxleyi B92/11	30, 300, 800	∩*	↑*	↑*	Trimborn et al. [96]
E. huxleyi CCMP 371	50, 400	→	↓	↓	Feng et al. [103]
E. huxleyi CS–369	150, 300, 500	↑*	∩*	∩	Xu and Gao [97]
G. oceanica NIES-1318	50, 190, 400	∩	↓	↓	Tong et al. [102]
E. huxleyi NIWA1108	14–650	↑*	→*	↓	Feng et al. [66]
E. huxleyi PML B92/11	80–480	↑	∩	∩	Zhang et al. [98]
E. huxleyi NIWA1108	50–1,000	→	↑	↑	Xi [71]

also declines with increasing UVR. Gao et al. [109] reported that UVR could inhibit *E. huxleyi*'s calcification rate by 45%, with UV-A and UV-B contributing 14% and 31%, respectively. Thus, we infer that higher UVR from a shallower oceanic mixed layer and ozone layer depletion reduces coccolithophores' PIC and POC production.

Nutrients

Nutrient levels govern phytoplankton growth, and cells' nutritional state impacts their photochemical capacity [110]. Climate-driven ocean warming exacerbates seawater stratification, impeding nutrient transfer from deeper waters to the surface layer and intensifying nutrient limitations for coccolithophore growth [80]. Calcification exhibits increased sensitivity to light and CO_2 levels when coccolithophores are limited by nutrients [111]. In nutrient limitation, cells prolong the G1 phase, which is the initial stage for calcification, typically resulting in an increased PIC:POC ratio [112]. In this regard, Paasche [113] reported that both nitrogen and phosphorus limitations resulted in an increase in total coccolith numbers for a cell, which can compensate for and even increase the cellular PIC quota as a potential loss in PIC may be caused by decreased calcite content per coccolith in N-limitation. Coccolithophores' remarkable nutrient uptake capacity gives rise to their critical role in the marine carbon cycle.

Phosphorus

Dissolved inorganic phosphate (DIP) plays a crucial geochemical role in marine ecosystems, supporting phytoplankton growth [114]. Marine phosphate originates from both natural and artificial sources. Natural phosphate encompasses biological lipids, nucleic acids, proteins, and polysaccharides, whereas synthetic phosphates primarily consist of herbicides and pesticides discharged into the sea [115–117]. Contrary to nitrogen in oceans, which can be replenished through biological nitrogen fixation, there is no similar source for marine phosphate. Consequently, DIP levels in the open ocean are exceptionally low—surface seawater phosphate exists only at nanomolar concentrations—making it an essential limiting factor for marine algal growth [118]. Phosphorus starvation leads to diminished phytoplankton growth rates and decreased CO_2 fixation via photosynthesis, theoretically resulting in a reduced capacity and efficiency of the BCP. However, coccolithophores have often been observed to form algal blooms in phosphorus-limited waters. For instance, Tanioka et al. found a positive correlation between high C:P ratio and coccolithophore abundance in polar and subpolar areas [119,120]. This suggests that certain adaptive strategies employed by coccolithophores can offset the diminished BCP capacity caused by slower growth rates and thus enhance carbon export efficiency.

Coccolithophores use various adaptive strategies under phosphorus-limited conditions. Coccolithophores can reduce phosphorus demand by restructuring cell membranes and facilitate phosphate release by up-regulating the transcription of phospholipase C and A [121]. The proportion of phospholipids in *E. huxleyi*'s cell membrane can decrease from 33% to 2%, concurrently minimizing its nitrogen requirement to prevent significant intracellular C/P fluctuations [122]. In this regard, Wang et al. [123] reported that under phosphorus-limited conditions, the up-regulation of C4 photosynthesis mRNA led to a 3.4-fold increase in POC content, a 5-fold increase in PIC content, and a 37% increase in coccolithophore sinking rate due to cell division inhibition. Müller et al. [112] also found that the Ca content of *E. huxleyi* was elevated by about 4-fold under P-limitation. Similar responses of PIC and POC contents were also presented in additional studies of *E. huxleyi* [67,113,124,125] and *Calcidiscus leptoporus* [126]. In laboratory conditions, coccolithophores under P-limitation often exhibit increased PIC:POC. This is attributed to the cells' inability to synthesize nucleic acids for cell division due to phosphorus scarcity, even as calcification persists [127].

Additionally, phytoplankton can utilize dissolved organic phosphorus to mitigate DIP deficiencies [128]. In the absence of DIP, *E. huxleyi* can utilize phosphorus-containing pesticides discharged into the sea, such as glyphosate, as its exclusive phosphorus source. Despite the low utilization efficiency of approximately 33%, attributed to energy costs and pesticide toxicity, *E. huxleyi* grown with glyphosate demonstrated an experimental increase in C content, C:P ratios, and sinking rate. The observed increase in cellular stoichiometry C and C:P suggests an enhanced carbon export per unit of phosphorus support, indicating improved carbon export efficiency of *E. huxleyi* [129].

Nitrogen

In marine environments, the accessibility of inorganic nitrogen sources such as NO_3^-, NH_4^+, and NO_2^- plays a crucial role in phytoplankton growth [130]. Increased stratification diminishes the nitrogen supply from deeper waters, whereas changes in pCO_2 substantially impact the marine nitrogen cycle, leading to a reduction in the NO_3^- to NH_4^+ ratio in seawater [131]. According to Feng et al. [66], N-limitation is predicted to be the most significant factor influencing the growth, photosynthesis, and calcification process of *E. huxleyi*.

N-limitation resulted in a reduction in growth rate [66,71,132,133] and chlorophyll *a* and *c* contents [134] and decreased efficiency in O_2 release through photosynthesis and HCO_3^- uptake during calcification [135]. Under nitrogen-limited conditions, the PON content of coccolithophores was reduced by one-third [135]. However, the carbon concentration mechanism regulated the rate of CO_2 fixation per unit of nitrogen by the Rubisco enzyme, maintaining a constant C:N ratio (8.3 to 8.5) in coccolithophores to ensure its adequate growth [135,136].

A decreasing trend in the POC content of *E. huxleyi* and *G. oceanica* was observed in various research [71,133,137,138], whereas *C. leptoporus* revealed the opposite trend [126]. Nonetheless, the impact of N-limitation on the PIC production of coccolithophores remains somewhat contentious. Through experiments with *C. leptoporus*, Langer et al. [126] demonstrated that this species could counteract nutrient stress by augmenting PIC production, as found in *G. oceanica* [133]. However, this was not corroborated in subsequent experiments with *E. huxleyi*. In response, Langer et al. [139] posited that the observed increase in PIC during the experiments could be attributed to variations in experimental methodology, asserting a lack of evidence to support the notion that N-limitation enhances particulate carbon export. Furthermore, akin to P-limitation, an upward trend was observed in the PIC:POC ratio of coccolithophores under nitrogen-limited conditions [71,126,127,135].

Guo et al. [138] and Xi [71] demonstrated that N-limitation led to a substantial decrease in the sinking rate of *E. huxleyi*. Meanwhile, according to Pantorno et al., *E. huxleyi* exhibited varying sinking rates at different growth stages. Specifically,

cells in the stationary stage sank faster under nitrogen-limited conditions compared with unrestricted cells, whereas cells in the exponential stage demonstrated a contrasting trend. In general, coccolithophores in the exponential stage exhibited the highest sinking rate under nitrogen-replete conditions [134]. However, Jiang et al. [133] found that N-limitation enhanced the sinking rate of *G. oceanica*. In contrast to Pantorno's view that cell size is the major factor that influences the sinking rate, he suggested that the ballast effect contributes more to POC sinking.

Iron

Iron is an essential element for all living things because of its ubiquitous presence in oxidoreductases and other enzymes, especially in respiration and photosynthesis [140]. Because the limited amount of iron in the ocean presents as highly insoluble minerals or polymeric oxidized hydrates [140], the open ocean contains less iron than most terrestrial environments, and the availability of iron has greatly restricted the primary production of marine phytoplankton [121]. When the iron concentration is reduced from 1,000 to 0 nM, the growth rate of coccolithophores decreases to one-third, whereas the carbon fixation efficiency concomitantly decreases [141]. However, coccolithophores can thrive even under limited iron availability, and blooms of coccolithophores have been observed in some iron-restricted areas. For instance, Muggli and Harrison discovered that *E. huxleyi* could sustain growth in naturally low-iron seawater while maintaining a constant cell size and a cellular C:N ratio. In contrast, diatoms ceased division after 3 generations [142]. Muggli and Harrison [143] found that iron limitation, while reducing the cell size of *E. huxleyi*, resulted in increased PIC and POC content and stabilized chlorophyll synthesis. The underlying mechanism of iron absorption remains to be investigated.

Combined effects of environmental factors

Marine organisms are exposed to complex and closely linked environmental factors. Multifactorial culture experiments have been conducted, which are essential and fundamental to understanding how the future marine environment may affect coccolithophores (Fig. 3).

Coccolithophores, as typical calcifying planktons, have drawn great attention from many scholars because of their susceptibility to OA. Thus, the interaction between acidification and various environmental factors has been extensively investigated. Liao et al. explored the impact of both dual and multifactorial interactions on the physiology and elemental composition of *E. huxleyi*, with a focus on OA. They found that the combined influences of acidification and nitrogen limitation synergistically reduced *E. huxleyi*'s PIC content while antagonistically decreasing its POC content. The sinking rate of coccolithophores was significantly reduced under high pCO_2–low N conditions [144]. Acidification and high light increased the POC content of *E. huxleyi* [101,145], which was further enhanced in a phosphorus-limited environment [145]. A combination of 5 factors, acidification, irradiance, temperature, nitrogen, and phosphorus, had the most significant negative synergistic effects on *E. huxleyi*'s physiology and elemental composition [146]. As discussed above, PIC:POC values were supposed to be increased under nitrogen and phosphorus limitation, but Rouco et al. [147] found that the addition of acidification decreased it. Changes in carbonate chemistry can also affect the bioavailability of micronutrients. Lorenzo et al. demonstrated that in current marine environments, increases in dissolved iron enhance *E. huxleyi*'s carbon fixation and stimulate coccolithophore bloom production. However, they projected that carbon production from coccolithophore blooms would be relatively lower in future marine environments modeled with increased pCO_2 levels [148].

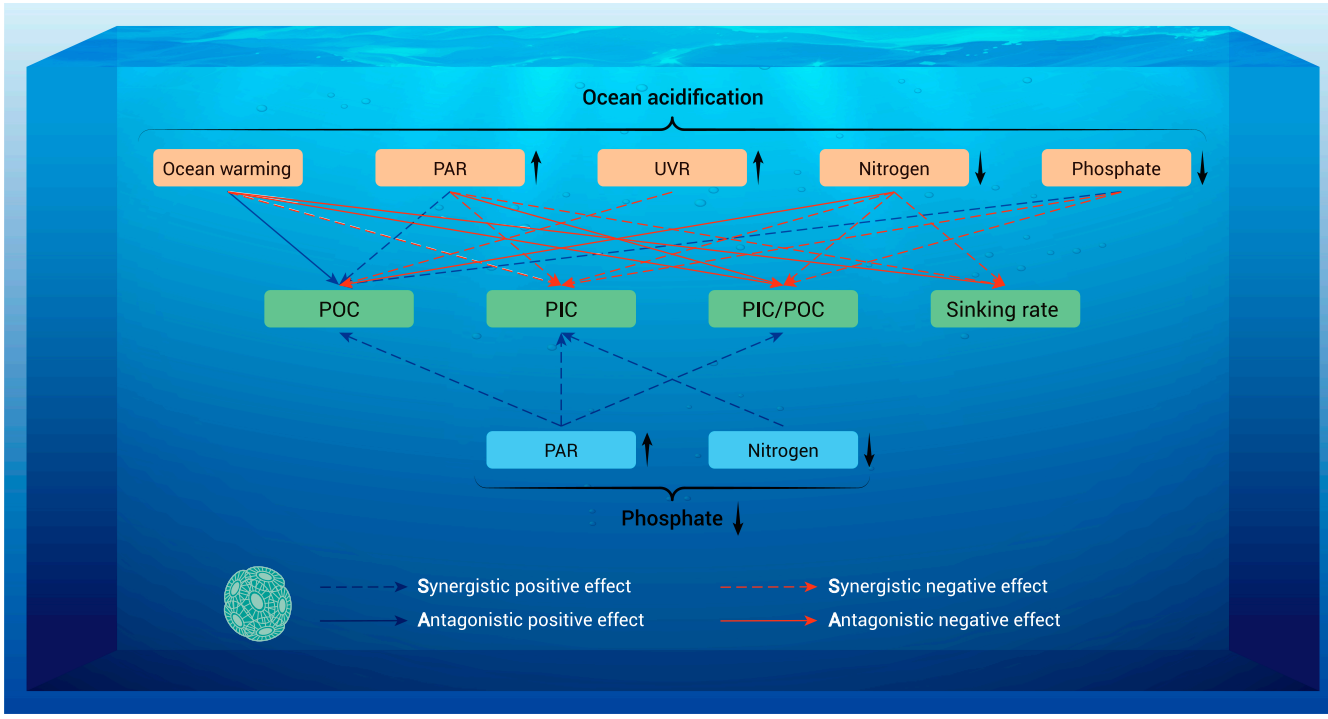

Fig. 3. Effects of multiple environmental factors on carbon accumulation and sinking rate of coccolithophores.

The extent to which coccolithophore PIC production responds to pCO_2 is usually dependent on temperature [149,150]. At optimal temperatures, increased heat can offset the adverse effects of high pCO_2. Milner's experiment showed that the combined effects of acidification and warming boosted *E. huxleyi*'s POC production rate [149]. Furthermore, the PIC:POC decrease in *E. huxleyi* resulting from increased pCO_2 became insignificant with rising temperature [149,150]. However, Sett concluded that the response of POC to pCO_2 was independent of temperature elevation, implying that high pCO_2 levels enhance POC production irrespective of thermal conditions [151]. The interplay between temperature and carbonate chemistry influences *E. huxleyi*'s density, subsequently reducing its sinking rate and diminishing carbon exportation [149]. Meanwhile, Jin et al. [152] examined how *G. oceanica*'s physiological traits (noncalcified strain domesticated for 400 generations under 1,000 μatm CO_2) respond to various environmental factors under greenhouse conditions. Their findings revealed an enhanced photosynthetic carbon sequestration capacity of *G. oceanica*, but survival pressures increased with UV radiation intensification.

Furthermore, the combined influence of light and diverse environmental factors has been extensively investigated. At a moderate light intensity of 150 μmol photons m^{-2} s^{-1}, the growth rate of *E. huxleyi* cultured with different nitrogen sources was substantially increased. Moreover, the sinking rate during the senescent phase was most significantly diminished under nitrate cultivation [137]. Increased light intensity and NO_3^--limiting conditions would have a significantly negative impact on the calcification of *G. oceanica* [102]. The joint impact of acidification (pH = 7.6) and UVR inhibited *E. huxleyi*'s calcification by 99% and photosynthesis by 15% [109]. The effectiveness of nitrogen sources played a crucial role in coccolithophore resistance to UVR exposure, with *G. oceanica*'s growth rates decreasing by 58% under both UVR exposure and nitrogen starvation [153].

Conclusions and Outlook

Coccolithophores are unicellular calcifying algae widely distributed across the global ocean. Through photosynthesis, coccolithophores contribute to the upper ocean BCP, accounting for up to 20% of total carbon fixation in unproductive central subtropical gyres [5]. Additionally, through calcification, they contribute to the CCP, and more than 50% of surface $CaCO_3$ sediments are derived from their contributions [6,154]. Environmental factors such as temperature, carbonate chemistry, and nutrient conditions are critical for the photosynthesis and calcification of coccolithophores, driving changes in their carbon accumulation and sinking, which, in turn, affects ocean–atmosphere CO_2 fluxes. The primary conclusions can be found in Fig. 4.

Studies involving field observations and laboratory cultures of coccolithophore carbon export have shown progress, yet the following challenges remain:

1. Previous studies mainly focused on the physiological parameters of coccolithophores in response to environmental factors. However, their molecular regulatory

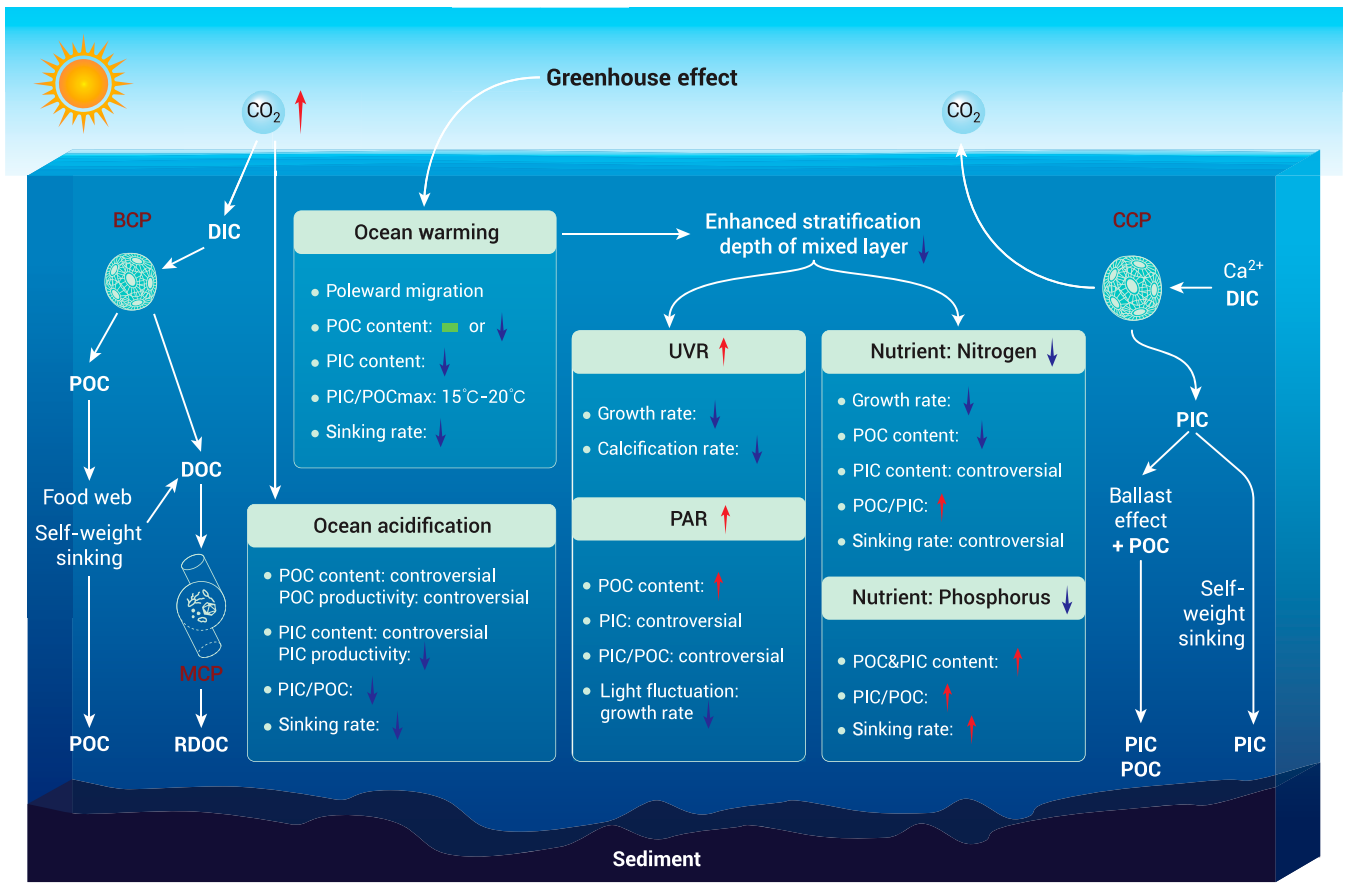

Fig. 4. Changes in carbon accumulation and sinking rate of coccolithophores under variable environmental factors.

mechanisms are yet to be discovered. A combination of transcriptomics, metabolomics, and other emerging research methods can help reveal the physiological responses of coccolithophores. This approach can also help investigate how key gene expressions and metabolic pathways change and clarify underlying regulatory mechanisms. Additionally, researchers should pay attention to the differences in carbon sequestration pathways between marine phytoplankton and land plants.

2. *E. huxleyi* is a common subject for studying the physiological response of coccolithophores to environmental change, but different species or strains of coccolithophores may have different response patterns [72,155,156]. In some areas, *E. huxleyi* does not contribute much to the export of PIC, so other species of coccolithophores should also be considered [7].
3. Indoor modeling experiments usually increase the mean temperature, but climate extremes may have caused more impacts than the average temperature [157]. Global warming affects the carbon export of coccolithophores through multifactorial interactions and biological adaptations, which are difficult to simulate in laboratory cultures. Therefore, short-term indoor domestication cultures, long-term acclimatization culture experiments, and large-scale and long-term field investigations should be integrated.
4. Field investigation of living coccolithophores in surface waters is a rising area of research. However, only a few studies have analyzed and compared the distribution patterns of living and dead coccolithophores in a short time scale. Combining the dynamics of planktonic communities with the accumulation rate of coccolithophores in the sediment surface layers can help estimate the actual export of coccolithophore carbon in the water column.
5. The study of carbon export by coccolithophores requires interdisciplinary research. Physical processes, such as mesoscale eddies, influence the carbon export of coccolithophores. Ocean color satellites can provide coccolithophore PIC data from surface water observations. However, satellite observations are more reliable in high-latitude, nutrient-rich waters than in nutrient-poor waters.
6. The coupling of BCP and CCP is the basis for studying coccolithophores. The ultimate goal is to understand how coccolithophores contribute to the oceanic carbon pump. Many studies have examined how environmental changes affect the PIC and POC export flux of coccolithophores, but the underlying biological mechanisms are still unclear. The contributions of coccolithophore PIC and POC export to the oceanic carbon export have not been precisely measured, and relevant models need improvement.

In summary, to estimate and predict the contribution of coccolithophores to the oceanic carbon pump under climate change accurately, further investigation and research are required. In-depth and systematic studies with multidisciplinary intersections are imperative.

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Data Availability

All data that support the findings of this paper are available in the references.

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