



## Meta-analysis reveals responses of coccolithophores and diatoms to warming

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### ABSTRACT

A meta-analysis was conducted to explore the effects of warming on the physiological processes of coccolithophores and diatoms by synthesizing a large number of published literatures. A total of 154 studies consisting 301 experiments were synthesized in this study. Under a projected temperature increase of 3–5 °C by IPCC AR6 at the end of this century, our results suggest that the growth and photosynthetic rate of coccolithophores were significantly enhanced by the rising temperature, while the calcification of coccolithophores was only slightly promoted. Warming also had significantly positive effects on the growth but not photosynthesis of diatoms. In comparison, the effect size of warming on the growth rate of coccolithophores was larger than that of diatoms. However, there was no significant effect of warming on either the ratio of particulate inorganic carbon to particulate organic carbon (PIC:POC) of coccolithophores or the ratio of biogenic silica to carbon (BSi:C) of diatoms. Furthermore, the results reveal latitudinal and size-specific patterns of the effect sizes of warming. For diatoms, the effects of warming on growth were more prominent in high latitudes, specifically for the Southern Hemisphere species. In addition, the effect size of warming on the small-sized diatoms was larger than that of the large-sized diatoms. For coccolithophores, the growth of the Southern Hemisphere temperate strains was significantly promoted by warming. Overall, the results based on the meta-analysis indicate that the projected warming of the end of this century will be more favor to the growth of coccolithophores than that of diatoms, thus potentially affect the competitive advantages of coccolithophores over diatoms; while the mid-to high latitude species/strains of both coccolithophores and diatoms will benefit more than their counterparts in the lower latitudes. Therefore, this study offers novel insights into predicting both the inter- and intra-group competitive advantages of diatoms and coccolithophores under the future warming climate change scenario.

### 1. Introduction

Marine phytoplankton, as the main primary producers in the ocean, contribute to nearly half of the global primary productivity and thus play crucial roles in the marine ecosystem and biogeochemistry (Field et al., 1998). In the recent decades, climate change induced by human activities causes substantial impacts on the marine ecosystem. Temperature rising is one of the most influential impacts. According to IPCC AR6 (SSP3-7.0 and SSP5-8.5), global surface temperature is predicted to increase by 3–5 °C by the end of this century (IPCC et al., 2022). The rise in temperature will have great impacts on the organisms in earth's ecosystem, and there is no exception for marine phytoplankton (Velthuis et al., 2022; Sheward et al., 2023; Edullantes et al., 2023; Bishop et al., 2022; Lewandowska et al., 2014; Petchey et al., 1999).

Temperature plays a pivotal role as a key environmental determinant in modulating enzymatic activities and metabolic rates of marine phytoplankton (Eisenthal et al., 2006). As a general trend, metabolic rates generally increase as temperatures rise until they reach an optimal temperature. However, once this optimal point is surpassed, further increases in temperature can have negative effects on metabolic rates. The specific temperature optimum for growth varies among different phytoplankton groups and species (Bestion et al., 2018). As such, numerous studies have suggested that the projected elevated temperature may have important impacts on the growth and photosynthesis of marine phytoplankton, with some groups benefited while some others weakened (Brandenburg et al., 2019; Lee et al., 2021; Rajadurai et al., 2005). Consequently, warming could result in changes in community structure of phytoplankton, further affecting the primary productivity

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and carbon export in the ocean (Godrijan et al., 2023; Thomas et al., 2012; Winter et al., 2014).

Due to the contribution to the biological carbon pump with ballast effect, coccolithophores and diatoms are among the best-studied marine phytoplankton functional groups (Reynolds et al., 2002; Weithoff, 2003). Coccolithophores, a group of marine haptophytes, are widely distributed in the global oceans (O'Brien et al., 2016). They are vital in the marine carbon cycle, contributing ~20% of the marine primary productivity and ~50% of the marine calcium carbonate production (Balch, 2018; Krumhardt et al., 2017). By conducting the carbonate counter pump (i.e., calcification), coccolithophores produce particulate inorganic carbon (PIC) in the form of calcium carbonate, decreasing seawater alkalinity and releasing CO<sub>2</sub> in the meanwhile. In addition, the coccoliths produced by coccolithophores can act as ballast material to accelerate the sinking of particulate organic carbon (POC) into deep layers (Beaufort et al., 2007). Diatoms, on the other hand, are the most diversified marine phytoplankton group, with an estimated over  $1 \times 10^5$  extant species (Kooistra et al., 2007; Mann, 1999), contributing nearly 40% of total oceanic production (Mann, 1999; Treguer et al., 2018). Marine diatoms generally dominate phytoplankton communities in the nutrient-rich coastal and upwelling regions (Morel and Price, 2003). With the capacity to form siliceous skeletons (frustules), diatoms make significant contributions to the carbon sinking and sequestration in the marine carbon cycle (Haese et al., 2007).

As two important functional groups of phytoplankton, diatoms and coccolithophores have been found to co-occur in the same marine regions and both can form blooms, suggesting a potential competitive relationship between them in situ. Synchronous or successive coccolithophore and diatom blooms have been observed in some oceanic and coastal regions, for instance, the North Atlantic, the Patagonian Shelf in the South Atlantic, the South African margin to the Antarctic shelf in the Indian Ocean (Godrijan et al., 2018; Balch et al., 2014; Barrett et al., 2018; Falkowski et al., 2003; Feng et al., 2009; Matson et al., 2019; Mikaelyan et al., 2015; Smythe-Wright et al., 2014; Vostokov et al., 2022). The availability of nutrients, light, and carbon dioxide concentration are factors that influence the community succession of coccolithophores and diatoms (Balch et al., 2014; Feng et al., 2009; Listmann et al., 2020; McCarthy et al., 2012; Poulton et al., 2014; Van Oostende et al., 2012). However, the impact of temperature is also highly significant (Godrijan et al., 2018; Anderson et al., 2021). Temperature may affect the growth, photosynthesis and biomineralization processes, thereby causing shifts in the dominance of different phytoplankton groups (Boyd and Doney, 2002; Litchman et al., 2010; Sett et al., 2014; Sheehan et al., 2020; Way and Yamori, 2014).

Warming impacts physiological processes in diatoms and coccolithophores, yielding diverse responses. Both coccolithophores and diatoms' growth rates rise due to accelerated metabolism, cell division, and photosynthesis under warming (Lopez-Urrutia et al., 2006). A 5°C temperature increase within the range of rising growth rates led some coccolithophore species (*Emiliania huxleyi*, *Gephyrocapsa oceanica*, and two strains of *Calcidiscus leptopus*) to increase their growth by about 50% (Buitenhuis et al., 2008). Notably, optimal growth temperature of *Emiliania huxleyi* is around 20 °C, potentially exceeding 22 °C (Zhang et al., 2014). Calcification rates increased within 10–15 °C for *Emiliania huxleyi* (Sett et al., 2014). The optimal growth temperature of marine diatoms varies between species (Barton et al., 2020); for example, *Thalassiosira pseudonana* (CS-20) grows optimally at 20.9 °C (Sheehan et al., 2020), while *Chaetoceros wighamii* Brightwell grows optimally at 28 °C (Rajadurai et al., 2005). Arctic diatom *Fragilaria barbararum*'s optimal is 12–14 °C (Karsten et al., 2006). Diverse diatom species (Anderson et al., 2021; Treguer et al., 2018) lead to intricate reactions. Some studies report decreased cellular biogenic silica (BSi) under warming, while others suggest heightened silicification (Kuefner et al., 2020; Pondaven et al., 2007; Sheehan et al., 2020). The impact of warming varies between diatoms and coccolithophores (Anderson et al., 2021; Seifert et al., 2020). Therefore, changes in temperature resulting from climate

change, seasonal transitions, and mixing can potentially alter the geographical distribution and succession of these two groups (Brun et al., 2015; Cerino et al., 2019; Henderiks et al., 2012; Kopelevich et al., 2015; Pinckney et al., 2015; Schiebel et al., 2004; Smith et al., 2017; Winter et al., 2014). Consequently, the relative geographic predominance of diatoms and coccolithophores, given their distinctive functions within marine biogeochemical cycles, carries considerable implications for the flux of carbon export and the cycling of nutrients (Falkowski et al., 2003).

Currently, a multitude of literature has been extensively published on the impacts of warming on coccolithophores and diatoms, encompassing diverse species and various data sets from different geographical regions. The ability to systematically integrate this vast amount of data using statistical methodologies to derive comprehensive outcomes is undoubtedly expected to greatly benefit future research endeavors. Meta-analysis is a standard tool to quantitatively synthesize the results of large amount of available data to estimate the overall state of knowledge in a specific area. With decades of development, meta-analysis has been considered as an important tool to make robust comparisons and improve the quality of evidence (Gurevitch et al., 2001). To generate reliable projections regarding the responses of coccolithophores and diatoms to environmental changes in the context of future global change scenarios, meta-analyses have been employed to assess the collective impacts of various individual environmental drivers. Some meta-analysis studies concerning coccolithophores have primarily centered on ocean acidification as the primary variable, while omitting temperature as a variable (Findlay et al., 2011; Meyer and Riebesell, 2015). A meta-analytical study has investigated the impact of temperature on the growth rates of several algal groups, including diatoms (Brandenburg et al., 2019), but did not specifically focus on coccolithophores and did not examine any indicators beyond growth rates. Several meta-analytical studies have investigated the impact of temperature on the growth rates of both coccolithophores and diatoms (Anderson et al., 2021; Seifert et al., 2020), but did not explore other indicators such as photosynthetic rates and biomineralization processes. However, photosynthesis, as the primary carbon fixation process, is crucial for sustaining marine ecosystems, while biomineralization is associated with vital processes such as oceanic carbon sequestration (Falkowski et al., 2003). Thus, conducting investigations into the temperature impacts on these processes holds substantial scientific significance.

In this study, we investigated the projected physiological responses of coccolithophores and diatoms to elevated temperatures by the end of this century by conducting a meta-analysis on the previously published results. The targeted physiological parameters include growth rate, photosynthetic rate, calcification rate, and the ratio of particular inorganic carbon to organic carbon (PIC:POC) for coccolithophores, and the ratio of biogenic silica to carbon (BSi:C) for diatoms. Extracted data were synthesized and subsequently compared to examine the warming effects, in order to answer the following questions: 1) What are the response to warming of different physiological parameters within the same phytoplankton functional group? 2) What are the differential or similar responses to the future warming trend between coccolithophores and diatoms? 3) How will these responses determine the distribution and competition of these two major phytoplankton functional groups?

## 2. Methods

### 2.1. Literature search and selection

Literature searches were performed in March to July 2022. The databases of Web of Science (<https://www.webofscience.com/>) and Scopus (<https://www.scopus.com/>) were scanned for literature to include in this study. The search queries in Table 1 were applied within article titles, abstracts, and keywords, yielding a total of 2628 literatures.

The screening process was illustrated using the PRISMA flow

**Table 1**

Search queries used in literature search process. In this table, 'a,' 'b,' 'c,' 'd' represent parts of the search sequence. The final search sequence format is "(a) AND (b) AND (c) AND (d)" (i.e., the keywords for a single search). IDs (C1, C2, C3, C4, D1, D2, D3) are used to simplify the representation of the single search sequences within the text.

ID	a	b	c	d
C1	marine	Coccolithophore	Growth Rate	Temperature OR Warming
C2	marine	Coccolithophore	"Photosynthetic rate" OR Photosynthesis OR POC OR "particulate organic carbon"	Temperature OR Warming
C3	marine	Coccolithophore	Calcification rate OR PIC OR "particulate inorganic carbon"	Temperature OR Warming
C4	marine	Coccolithophore	(PIC OR "particulate organic carbon") AND (POC OR "particulate organic carbon")	Temperature OR Warming
D1	marine	Diatom	Growth Rate	Temperature OR Warming
D2	marine	Diatom	"Photosynthetic rate" OR Photosynthesis OR POC OR "particulate organic carbon"	Temperature OR Warming
D3	marine	Diatom	((BSi OR Si) AND C) OR (silic* AND carbon*)	Temperature OR Warming

diagram for new systematic reviews (Page et al., 2021) (Fig. 1). At the first selection step (Screening Step I), titles and abstracts of articles were reviewed. Studies meet any of the criteria below were excluded: (1) Non-target species: target species of studies are not coccolithophores or diatoms, or only freshwater species were included; (2) Non-target indicators: target indicators of studies did not include growth rate, photosynthetic rate, calcification rate or required element ratio; (3) Non-target conditions: experimental conditions did not include temperature change; (4) No primary data: studies did not provide primary data (reviews, modeling, etc.); (5) Language issues: studies were not written in English; (6) Temporal issue: paleoceanographic research; (7) Non-laboratory: studies based on field data or mesocosm experiments. However, the review articles in (4) were retained, and their reference lists were manually screened to avoid the possibility of missing any relevant citations (Retrieving). The remaining articles from the first step of screening (Records screened in Fig. 1) proceed to the second step of screening (Screening Step II). In the second selection step, the full articles were reviewed. Studies meet any of the criteria below were excluded: (1) Experimental design: temperature could not be separated as a single variable or other conditions ( $p\text{CO}_2$ , pH, etc.) are out of ambient range. For example, the original text explicitly stated that temperature experiments were not conducted under conditions representative of the present day, or the values in their control group were not within the scope of interest. Specifically, the control group's  $p\text{CO}_2$  and pH ranges exceeded  $400 \pm 100$  ppm and  $8.0 \pm 0.5$ , respectively; or the light and nutrient levels in their control group were inappropriate, inhibiting the growth of specific algal strains (which may vary depending on the particular strain); (2) Missing outcomes: unknown standard deviation or unreported sample number; (3) Mixed population: target species are not single species or data of single species could not be separated.

After Step II, the bibliographies of leftover studies and bibliographies of Step I (4) were kept as another studies base (Retrieving Base). Duplicate removal and keyword searching were performed first using Endnote 20 software. Then Step I and Step II were repeated in Retrieving Base for screening. At the end of the screening, a total of 157 articles were included in the final selection, consisting of 65 articles on coccolithophores and 92 articles on diatoms. For specific quantities of literature related to each indicator, please refer to Fig. 1.

## 2.2. Data extraction

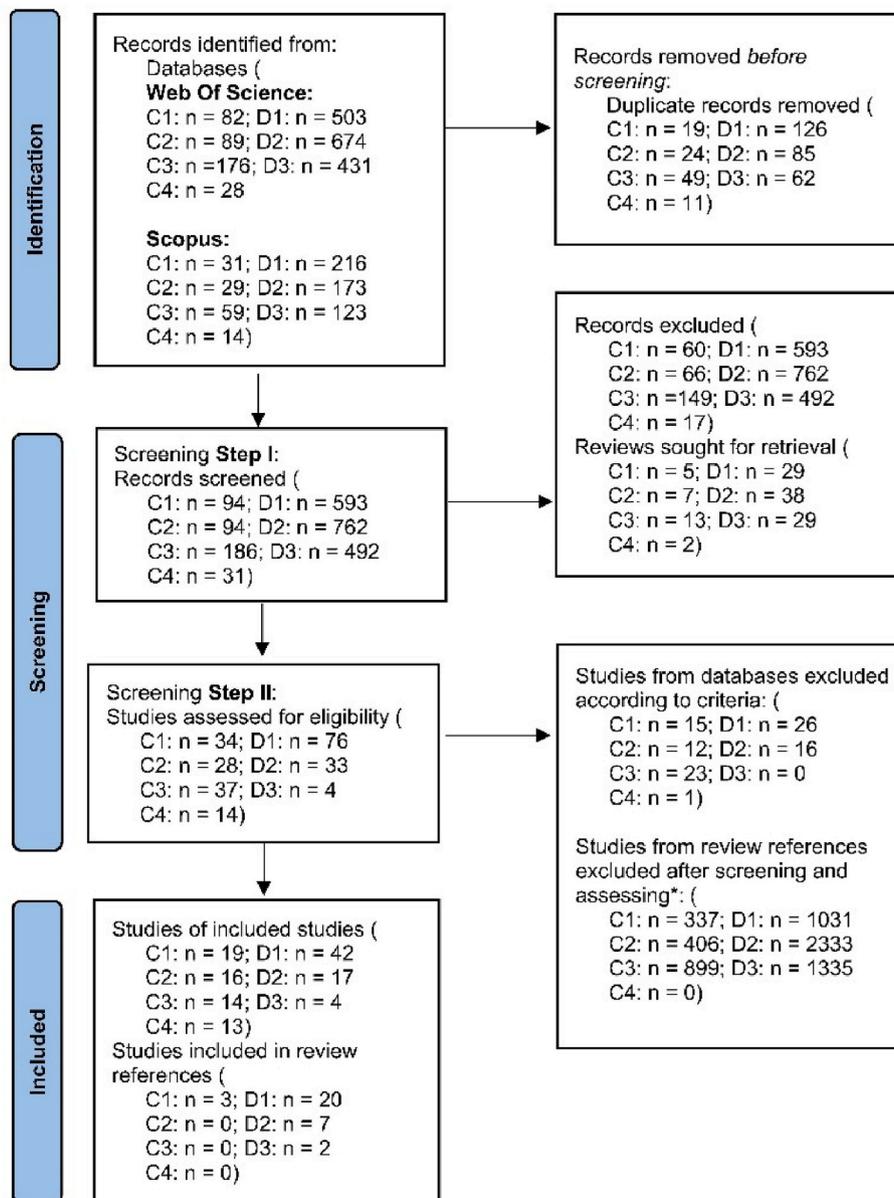
The following information was also recorded: author, published year, DOI, data type, species, strain code, strain origin, experimental light intensity, medium,  $p\text{CO}_2$ , annual average temperature range of strain origins, and volume of diatom cells. The diatom cell volume data that were not reported in the original studies were acquired either through the Nordmicmicroalgae database (URL: <http://nordmicmicroalgae.org/>) or through a literature search. Additionally, this study utilized Algaebase (<https://www.algaebase.org/>) and mentioned algal repositories in original studies to verify taxonomic synonyms and strain identifiers, ensuring that the same species and strains were not redundantly recorded. For diatoms, both single-celled and chain-forming species were included. However, this study did not impose restrictions on the original experiment's acclimation and cultivation periods.

In a meta-analysis, the control group and experimental group must be identified for evaluating the effect size of a particular variable. In this study, that variable is temperature, making it crucial to determine the respective temperatures for control and experimental groups. The experimental group temperature which represents the projected seawater temperature in the future, was set higher than that of the control group, which represents the present seawater temperature. According to the IPCC AR6 (2022), the temperature difference between the control and experimental groups was set to fall within the range of 3–5 °C.

In this context, we gave preference to the control and experimental group temperatures explicitly provided in the original text, ensuring they remain within this 3–5 °C warming range. If the original text did not specify the control and experimental group temperatures, especially in cases with multiple temperature settings, we used the temperatures for stock culture maintenance mentioned in the original text or those from algal culture repositories such as the Bigelow NCMA and the Roscoff Culture Collection for the control group temperature. The experimental group temperature was then selected from within the 3–5 °C warming range. If neither of the two types of information was available in the original text, we turned to using the original isolation temperature of the algal strains. The temperatures of strain origins were determined using data from The World Ocean Atlas (WOA) (<https://www.ncei.noaa.gov/products/world-ocean-atlas>) and [seatemperature.org](https://seatemperature.org). The experimental group temperature was still chosen to be within the 3–5 °C warming range from the control group.

The environmental conditions, apart from temperature, should be maintained at ambient/optimal levels. Apart from temperature variables, if the original study did not control for other variables such as light intensity, nutrients, light-dark ratios, etc., this study compared the maintenance conditions with those mentioned in the original research and the algal repositories, such as Bigelow NCMA (<https://ncma.bigelow.org/>) and The Roscoff Culture Collection (<https://roscoff-culture-collection.org/>), to confirm that none of the original study's variables became limiting factors before selecting it for reference. If the original study incorporated variables like light irradiance and trace elements, this study selected conditions closest to the stock culture conditions. To ensure the absence of growth limitations, a group with higher nutrient or light intensity levels would be selected within a close gradient. In experiments involving seawater acidification, this study uniformly chose the carbonate system configuration mentioned in the text as the control condition (simulating current conditions, with  $p\text{CO}_2$  typically controlled at ~400 ppm). However, no additional restrictions were applied to the control group's carbonate system. These approaches ensure that temperature remains the sole variable capable of influencing the physiological state of the target species or study group to the greatest extent possible.

Then, data on growth rate, photosynthetic rate, calcification rate (of coccolithophores), PIC:POC (for coccolithophores) and BSi:C (for diatoms) were extracted from each selected study. Regarding growth rates, data from the exponential growth phase were selected. Data that



**Fig. 1.** PRISMA flow diagram of this study. \*The process of selecting reference articles within the review is the same as the general process; therefore, it is not explicitly detailed in the diagram. Please refer to [Table 1](#) for the IDs (C1–4, D1–3) of each screening group.

includes standard deviation and sample numbers were directly extracted from original studies. Data reported in the forms of graphs were extracted using WebPlotDigitizer (Version 4.5, Ankit Rohatgi, <https://automeris.io/WebPlotDigitizer>).

Specifically, there are three different methods for measuring photosynthetic rate in selected studies: a)  $POC \times \mu$  (multiplication of cellular Particulate Organic Carbon content by growth rate) b) Unit time carbon transfer measured through isotopic analysis ( $^{14}C$  incubation technique). c) Oxygen evolution per unit time. If the original article did not provide photosynthetic rate data but provides raw data for growth rate and cellular POC content, photosynthetic rate data was manually calculated using method (a). Similarly, within the selected literature, there are also two methods for measuring the rate of calcification: a)  $PIC \times \mu$  (multiplication of cellular Particulate Inorganic Carbon content by growth rate) b) Unit time carbon transfer measured through isotopic analysis (The  $^{14}C$  incubation technique). When necessary, the rate of calcification could also be manually calculated. These methods are widely accepted in published literature (References for calculating

calcification rates (or photosynthesis rates) by multiplying with  $\mu$ , PIC (or POC), include but are not limited to: [Fiorini et al., 2011](#); [Klitzsch et al., 2020](#); [Matson et al., 2016](#); [Langer et al., 2009](#); [Cai et al., 2022](#); [Passow and Laws, 2015](#)). Furthermore, after calculating the effect sizes, the effects can be measured in a dimensionless and standardized manner. Therefore, this study did not differentiate between these methods individually.

In the analysis of latitudinal patterns, the latitudes were divided into six groups in three ranges: low (0–30°S and 0–30°N), middle (30–60°S and 30–60°N) and high (60–90°S and 60–90°N) latitude regions according to [Seifert et al. \(2020\)](#). However, the latitudinal distribution of coccolithophores is uneven compared to diatoms, with a greater presence in mid-latitude regions. In the analysis of diatom size classes, the cell sizes of diatoms were divided into two distinct groups: ‘Small diatoms’ with cell volumes less than 1000  $\mu m^3$ , and ‘Large diatoms’ with cell volumes greater than 1000  $\mu m^3$ . Using 1000  $\mu m^3$  as a threshold to categorize diatom size not only ensures that the physiological differences among diatoms of different sizes, such as variations in surface area

leading to differences in growth and photosynthetic activity, as well as differences in abundance and biomass, can be well represented but also ensures a certain degree of data concentration within both size intervals (Snoeijs et al., 2002; Zhang and Luo, 2022).

The included references and data can be found in supplementary information (Appendix A).

### 2.3. Data analysis

#### 2.3.1. Effect size

Logarithmically transformed response ratio ( $L$ ) was applied as the effect size. In ecological meta-analysis, it is a commonly employed effect size (Koricheva et al., 2013). In comparison to another prevalent effect size, the standardized mean difference, it holds greater practical significance (Hedges et al., 1999).

$L$  was calculated as:

$$L = \ln \frac{\overline{X}_E}{\overline{X}_C}$$

where  $\overline{X}_E$  and  $\overline{X}_C$  represents the mean value of experimental and control groups, respectively.

The variance  $v$  of each effect size  $L$  was calculated as:

$$v = \frac{S_E^2}{n_E \overline{X}_E^2} + \frac{S_C^2}{n_C \overline{X}_C^2}$$

$n_E$  and  $n_C$  represents the sample size of experimental and control groups in a particular study;  $S_E$  and  $S_C$  are the standard deviation of experimental and control groups, respectively.

When the value of  $L$  is less than zero ( $L < 0$ ), the effect in the treatment group has a negative effect. Conversely, when the value of  $L$  is greater than zero ( $L > 0$ ), the effect of warming in the treatment group is positive. A response ratio of zero ( $L = 0$ ) suggests that there is no effect, implying that the responses in both the control and treatment groups are identical. In this study, positive represents “promote” while negative represents “inhibit” in biological meaning.

The random effects model was employed to calculate the mean effect size and confidence intervals. If the 95% confidence interval does not include zero, the mean effect size is considered significant.

When a study has relatively higher precision, it should be considered more important. Giving studies with higher precision higher weights ( $\omega$ ) is an effective way. To attain this goal, the inverse-variance weighting method was used. Weight of study  $k$  ( $\omega_k$ ) is calculated as:

$$\omega_k = \frac{1}{\sigma_k^2 + v_k}$$

$$L^* = \frac{\sum_{k=1}^K \omega_k L_k}{\sum_{k=1}^K \omega_k}$$

where  $k$  represents number  $k$  study of all studies;  $K$  is the total number of all studies;  $L^*$  is the weighted effect size.  $\sigma^2$  is the between-study heterogeneity. The above formulas were based on the article by Hedges et al. (1999).

#### 2.3.2. Heterogeneity and sensitivity analyses

The random-effects model with the restricted maximum likelihood (REML) estimator was applied in this study to test heterogeneity  $\tau^2$ . When homogenous assumption is rejected, a positive estimate of  $\tau^2$  is produced. Therefore, a larger standard error and wider confidence interval for  $L^*$  is produced. By that means, an overall effect size of all studies included could be computed.

To test the robustness of the study, we employed a sensitivity analysis approach (Kroeker, K. et al., 2010). Sensitivity analysis is utilized to

investigate the influence of experiments that exhibit exceptionally large effect sizes. This process involves sorting each experiment based on the magnitude of its effect, then gradually excluding experiments with the largest effects (regardless of their direction) and reanalyzing the data. Considering that data points with smaller effect sizes also tend to contribute less to the overall effect, we sequentially removed the ten data points with the largest effects for testing purposes. Meanwhile, the ‘rstudent’ function in the ‘metafor’ package in R was used to check the standardized residuals. If a data point exhibits a significant deviation from other samples and, simultaneously, has a large residual value, it is an outlier that may be considered for removal. (Viechtbauer, 2010). Besides, if a study had a sample size exceeding 5, it was also excluded, and the analysis was then re-conducted. If it did not affect the significance, the study was retained. We also conducted Rosenthal’s fail-safe number test on significant effect sizes to determine the potential number of non-significant studies that might be concealed. When Rosenthal’s fail-safe number exceeds  $5k+10$ , it indicates the effectiveness of the significance of the effect size ( $k$  represents the number of effect sizes) (Rosenthal 1979).

All the data analyses were performed using “metafor” package (Version 3.8–1) (Viechtbauer, 2010) in R version 4.2.1 (R Core Team, 2022).

The calculated individual effect values can be found in the supplementary information (Appendix B).

## 3. Results

### 3.1. Overall effect sizes

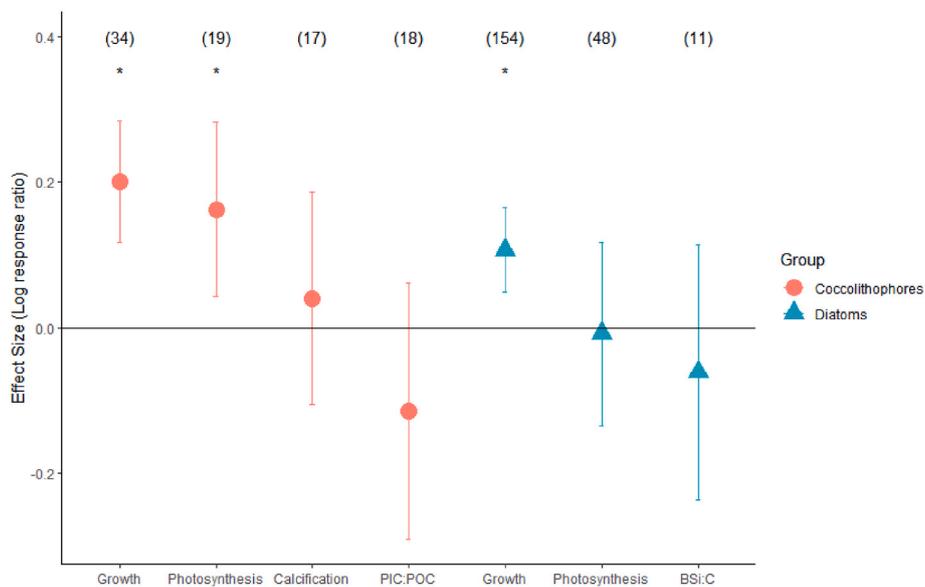
Our meta-analysis reveals significant positive effects of warming on the photosynthetic rate of coccolithophores and the growth rate of diatoms (Fig. 2). For coccolithophores, there was a positive and significant effect of warming on the growth rate ( $L^* = 0.2010 \pm 0.0835$ ,  $n = 33$ ). Additionally, a significant positive effect of warming on the photosynthetic rate was observed ( $L^* = 0.1626 \pm 0.1204$ ,  $n = 19$ ). The effect of warming on the calcification rate ( $L^* = 0.0401 \pm 0.1462$ ,  $n = 17$ ) and PIC: POC were non-significant. For diatoms, a significant overall positive effect size was observed on the growth rate ( $L^* = 0.1067 \pm 0.0584$ ,  $n = 154$ ). Nevertheless, the absolute mean effect size (0.1067) was smaller than that of coccolithophores (0.2010). In contrast to that of coccolithophores, the mean effect size on photosynthetic rate of diatoms was negative, and with the CI overlapping zero ( $L^* = -0.0086 \pm 0.1261$ ,  $n = 48$ ). Similarly, the effect of warming on BSi:C was not significant, showing a negative mean effect size ( $L^* = -0.0617 \pm 0.1759$ ,  $n = 11$ ).

### 3.2. Effect sizes associated with latitudinal groups

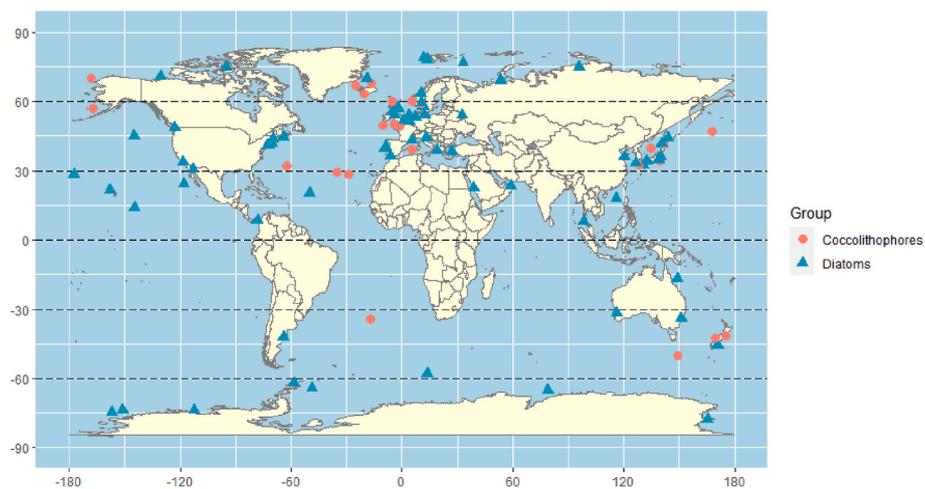
The origins of the species/strains included in this study cover a wide latitudinal range (Fig. 3, Appendix A). The majority of studies on coccolithophores collected in this study focused on *Emiliana huxleyi* (~81%, 30 out of 37 observations). In addition to *Emiliana huxleyi*, four other species, namely *Coccolithus braarudii* ( $n = 1$ ), *Coccolithus pelagicus* ( $n = 2$ ), *Gephyrocapsa oceanica* ( $n = 1$ ) and *Gephyrocapsa ericsonii* ( $n = 1$ ), were also included in the studies, albeit in smaller sample numbers. Therefore, the results of coccolithophores are primarily distributed among different strains of *Emiliana huxleyi*. This study includes over 100 species of diatoms (Appendix A). Therefore, the data of diatoms primarily distribute among different species. These diatoms were further categorized based on cell volume, such as *Thalassiosira pseudonana* (~150  $\mu\text{m}^3$ ), *Phaeodactylum tricorutum* (~150  $\mu\text{m}^3$ ) (Small diatoms); *Coscinodiscus concinnus* (> 1 000 000  $\mu\text{m}^3$ ), *Thalassiosira weissflogii* (> 1000  $\mu\text{m}^3$ ) (Large diatoms).

#### 3.2.1. Coccolithophores

The effect sizes associated with latitudinal variability on coccolithophores are shown in Fig. 4. The effects of warming on growth in



**Fig. 2.** Summary plot showing overall effect sizes of warming on coccolithophores and diatoms. The numbers in parentheses indicate the number of experiments used for calculating the effect sizes. The error bars represent the 95% confidence intervals. An asterisk (\*) indicates a significant response, which is determined when the confidence interval does not overlap zero. The zero line indicates no effect.



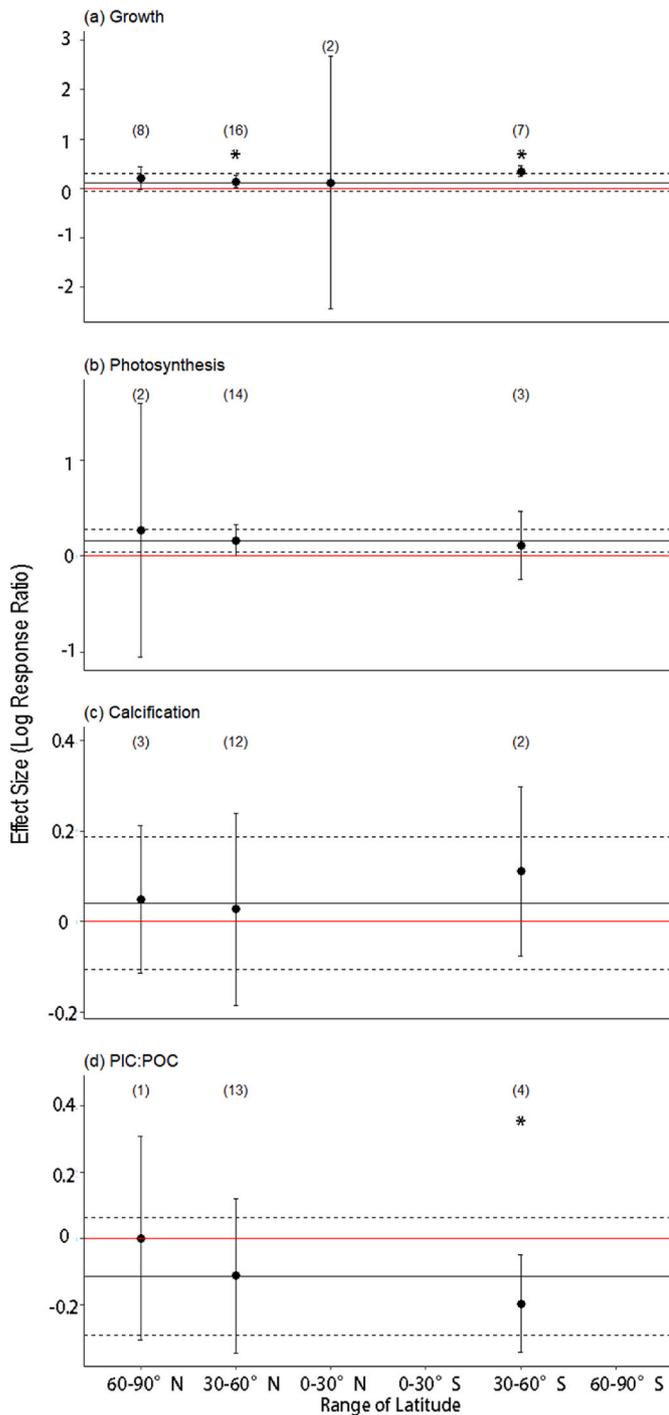
**Fig. 3.** Distribution of isolation sites of the coccolithophore and diatom species/strains in this study. The detailed information of the species/strains and the isolation sites is provided in Appendix A.

Northern Hemisphere regions was non-significant (Appendix B, Fig. 4a). The effect sizes of the coccolithophores isolated from the Northern Hemisphere middle-latitude (30°S–60°N) ( $L^* = 0.1393 \pm 0.1240$ ,  $n = 16$ ) and the Southern Hemisphere middle-latitude (30°S–60°S) ( $L^* = 0.3467 \pm 0.1096$ ,  $n = 7$ ) were positive and significant, with narrow CIs, indicating relatively homogenous results. The effect sizes of warming on the photosynthetic rate in different regions were all positive but non-significant (Fig. 4b, Appendix B). The effect of warming on the calcification rate and PIC:POC in different regions were also non-significant (Fig. 4c and d, Appendix B), except for PIC:POC in the mid-latitude region in the Southern Hemisphere ( $L^* = -0.1968 \pm 0.1473$ ,  $n = 4$ ).

### 3.2.2. Diatoms

For the growth rate of diatoms, isolated from the Northern Hemisphere middle-latitudes (30°N–60°N) ( $L^* = 0.1157 \pm 0.1017$ ,  $n = 73$ ) as well as in both northern and southern high-latitudes (in 60°N–90°N:  $L^* = 0.1251 \pm 0.1064$ ,  $n = 23$ ; in 60°S–90°S:  $0.2989 \pm 0.1227$ ,  $n = 14$ ), the effects of warming on the growth of diatom were positive and significant (Fig. 6a). Growth rate in high-latitude regions show a stronger

positive response to temperature increase compared to mid-latitude regions (in 30°N–60°N:  $L^* = 0.1157 \pm 0.1016$ ,  $n = 73$ ; in 30°S–60°S: non-significant, see Appendix B) and low-latitude regions (non-significant, see Appendix B). Regarding the photosynthetic rate of diatoms, on the whole, the mean effect sizes of Southern Hemisphere species were higher than those in all latitudinal groups in the Northern Hemisphere (see Appendix B). Furthermore, the only significant result is found in the high latitudes of the Southern Hemisphere ( $L^* = 0.5435 \pm 0.0878$ ,  $n = 3$ ). The photosynthetic rate of species isolated from the high latitudes of the Southern Hemisphere exhibits a more positive response to temperature increase than that of species from mid and low-latitude regions (which is non-significant). However, it is important to note that the sample size in the southern hemisphere regions was relatively smaller (Figs. 6b and 7b). Similar to the PIC:POC of coccolithophores, the effect sizes of warming on BSi:C were generally not significant (Appendix B). Although the mean effect size in the Southern Hemisphere high-latitude (60°S–90°S) was significant, it is important to note that the sample size was too small ( $n = 1$ ) to accurately represent the responses of strains in the high latitudinal region of the southern hemisphere (Figs. 6c and 7c,

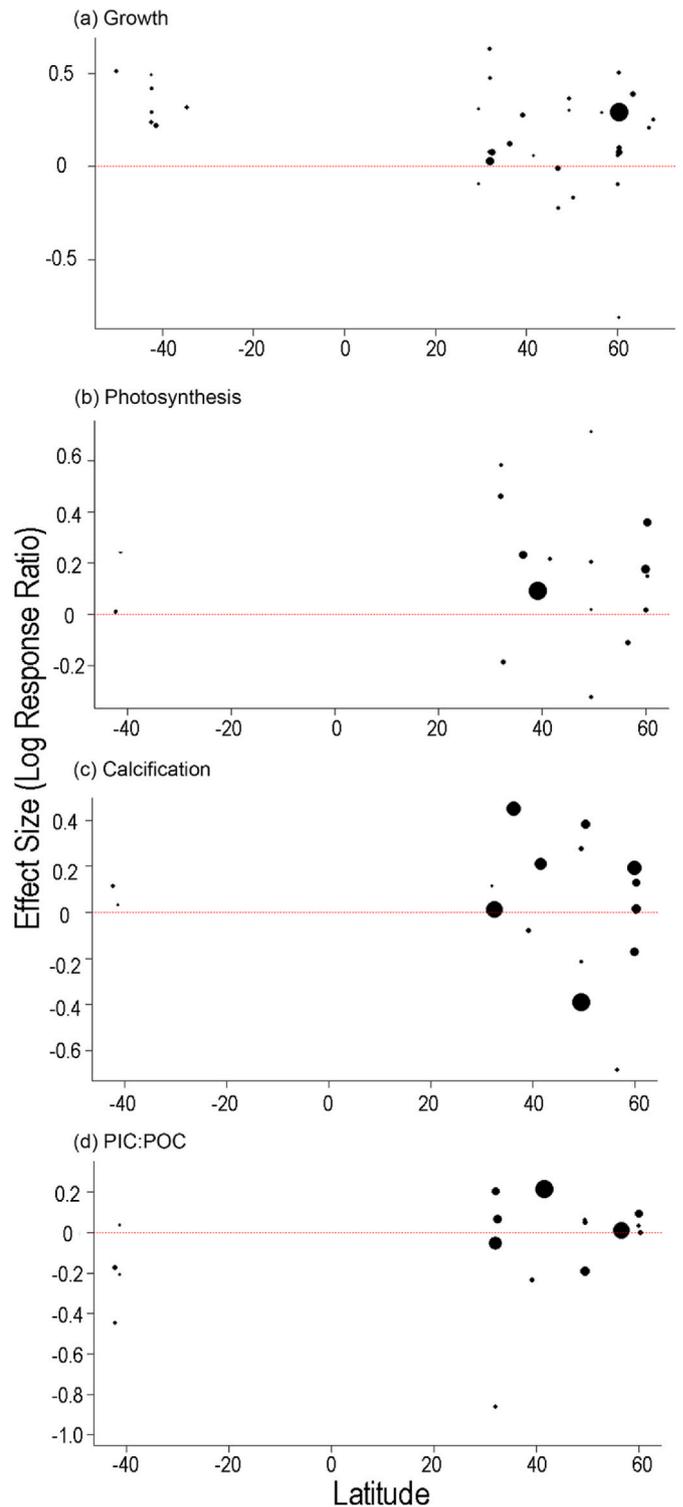


**Fig. 4.** The effects sizes of warming on coccolithophores across different latitudinal ranges: (a) Growth; (b) Photosynthesis; (c) Calcification; (d) PIC:POC. The numbers in parentheses indicate the number of studies included in the calculation. The black solid horizontal line in each graph represents the overall effect size of all coccolithophore strains. The black dashed lines indicate the confidence interval for the specific effect size. The red solid line represents zero (no effect). An asterisk (\*) indicates a significant response.

Appendix B).

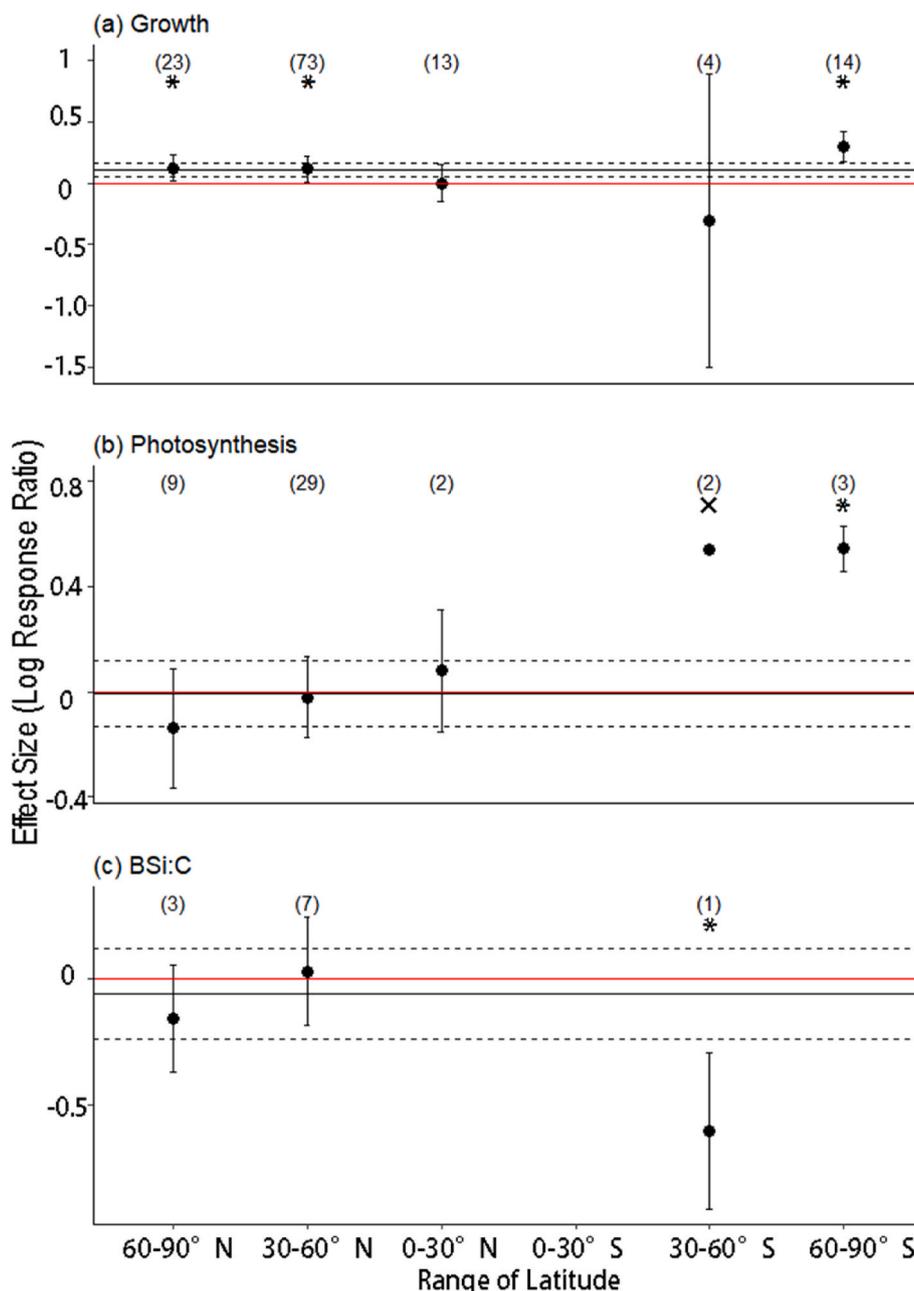
### 3.3. Effect sizes associated with diatom sizes

Effects of different sizes of diatom cells was also investigated (Figs. 8 and 9). The results suggest that warming prompted the growth of small sized ( $L^* = 0.1409 \pm 0.0887$ ,  $n = 79$ ) class to a larger extend than that of



**Fig. 5.** Data distribution plot of log response ratio of: (a) growth; (b) photosynthesis; (c) calcification; (d) PIC:POC to warming on coccolithophores as a function of latitude. The radius of each circle corresponds to the weight (inverse of variance) of the respective data point. The red dashed line indicates no effect.

large sized diatoms ( $L^* = 0.0515 \pm 0.1047$ ,  $n = 49$ ) (Fig. 8a). The effect of warming was not significant on the photosynthetic rate of small-sized diatoms ( $L^* = 0.0601 \pm 0.2700$ ,  $n = 19$ ) (Fig. 8b). In contrast, the photosynthesis of large-sized diatoms appeared to be inhibited by warming, as indicated by the upper boundary of the effect size confidence interval being very close to 0 ( $L^* = -0.1488 \pm 0.1494$ ,  $n = 17$ )



**Fig. 6.** The effects sizes of warming on diatoms across different latitudinal ranges: (a) Growth; (b) Photosynthesis; (c) BSi:C. The number of experiments included in the effect size calculation is presented in parentheses. The black horizontal solid line in each graph indicates the overall effect sizes of all strains of diatoms for the specific effect size. The black dashed lines indicate the confidence interval of the specific effect size. The red solid line indicates zero (no effect). An asterisk (\*) indicates a significant response. × represents the CI not shown here due to relatively large value (−8.1961 to 9.2746).

(Fig. 8b). The effects on the BSi:C of diatoms in both size classes were non-significant (Fig. 8c, Appendix B).

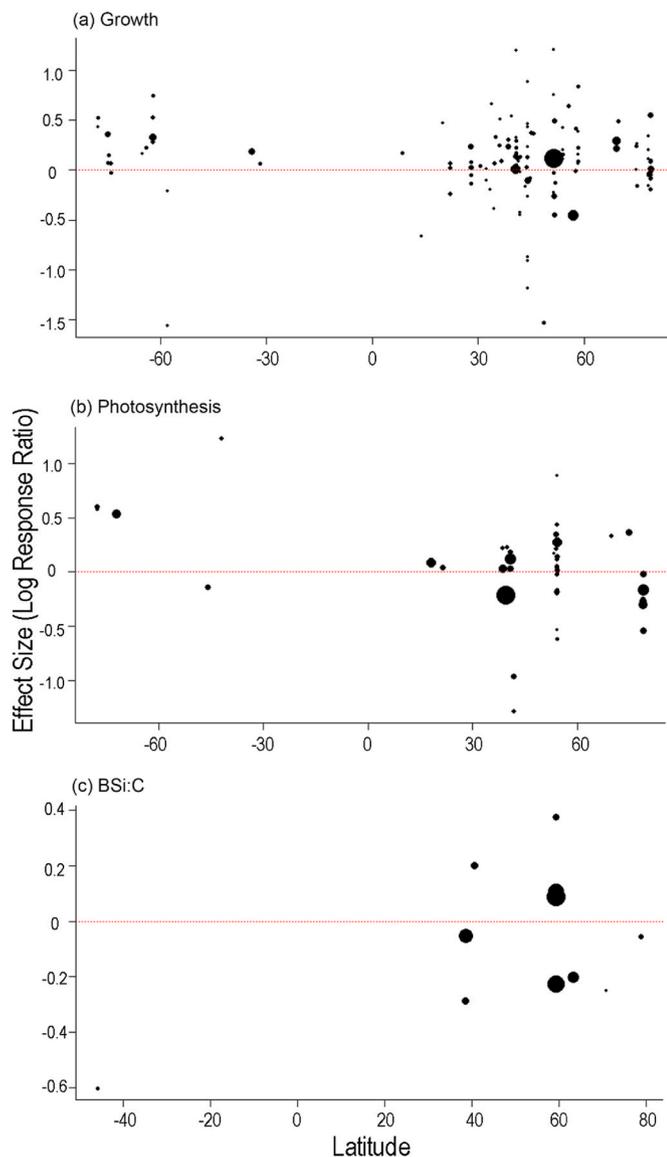
### 3.4. Sensitivity analyses

In one study (Langer et al., 2009) an observation (strain RCC1238), related to coccolithophore growth rates was excluded from all analyses as part of the sensitivity analysis (see Appendix C). The study's effect size is the largest in absolute terms; its removal alone changed the significance. Subsequently, removing 10 data points in order of their effect size did not alter the overall direction and significance of the effect. Regarding coccolithophore photosynthesis, it required the removal of 10 data points (50% of the data points) to change the significance. The sequential removal of 10 data points for coccolithophore calcification,

PIC:POC, and diatom growth rate and photosynthesis rate did not change the significance. Due to the limited number of data points for diatom BSi:C (11 data points), only 8 data points were sequentially removed, and the significance did not change. Studies with a sample size exceeding 5 did not impact the obtained results. In addition, the calculated Rosenthal's fail-safe numbers range from 1261 to infinite, which is quite high. The above results essentially ensure the robustness of this study.

## 4. Discussion

The study synthesized available data using a meta-analysis method and revealed a general pattern of physiological responses of coccolithophores and diatoms under future warming scenario projected for the



**Fig. 7.** Data distribution plot of log response ratio of: (a) growth; (b) photosynthesis; (c) BSi:C to warming on diatoms as a function of latitude. The radius of each circle corresponds to the weight (inverse of variance) of the respective data point. The red dashed line indicates no effect.

end of this century. This approach provides a comprehensive comparison of the potential responses between the two phytoplankton functional groups under warming. Additionally, the geographical and species-specific effects were examined by conducting comparisons between different latitudinal regions and size classes.

In the preliminary stages, we hypothesized that warming would significantly increase the growth rate and photosynthetic rate of both coccolithophores and diatoms with a less pronounced response in biomineralization. Furthermore, we predicted that diatoms' positive response to warming would be slightly weaker compared to coccolithophores. The results of this study largely align with our expectations. However, the response of diatom photosynthesis to warming was lower than anticipated, as it was not statistically significant.

In general, the growth and photosynthesis of coccolithophores were promoted to a larger extent compared to diatoms, indicating that coccolithophores may benefit more than diatoms in a warmer environment. Meanwhile, the effects size of warming on growth and photosynthesis were larger compared to those on the biomineralization indexes (calcification, PIC:POC, and BSi:C). The mean effects on PIC:POC of

coccolithophores and BSi:C were negative, suggesting a potential decrease on the biomineralization of both groups by warming, thus affecting the consequent biogeochemistry (Balch et al., 2010).

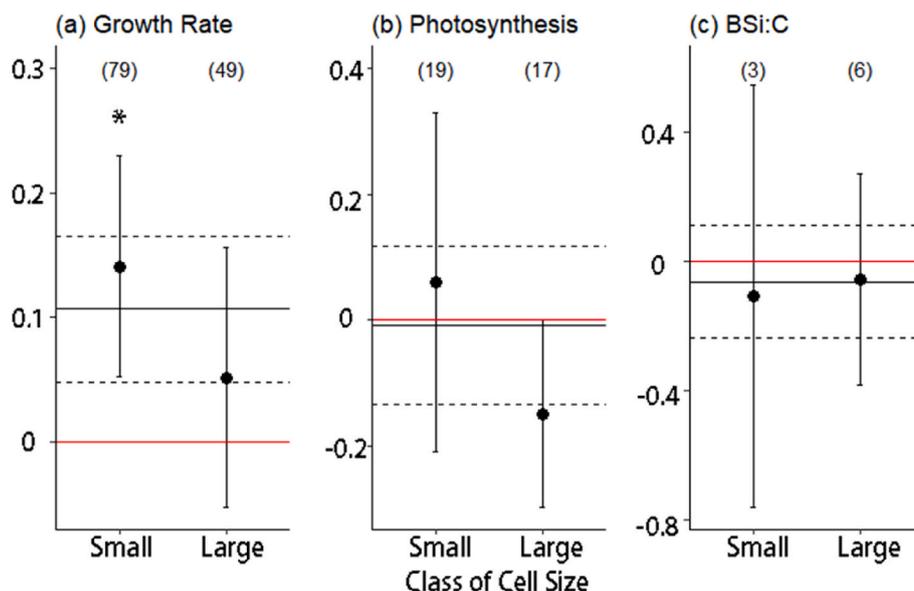
#### 4.1. Coccolithophores

##### 4.1.1. Growth, photosynthesis and biomineralization of coccolithophores

Overall, our results are biased towards *Emiliana huxleyi*, but not entirely. The effect size of coccolithophore growth exceeded that of diatom growth, indicating that warming has a significantly positive effect and a greater magnitude of impact on the growth of coccolithophores. This result aligns with the findings regarding coccolithophore growth rates in the meta-analyses and simulations conducted by Seifert et al. (2020), Krumhardt et al. (2017), Sheward et al. (2023) and Harvey et al. (2013). This could be due to the fact that *Emiliana huxleyi*, the species contributing significantly to the research findings, has a higher optimal growth temperature (Fielding, 2013). The annual average temperatures in the actual habitats of many coccolithophore species are lower than the temperatures required for these species to achieve their respective maximum growth rates (Chen, 2015; Langer et al., 2009; Rosas-Navarro et al., 2016; Sett et al., 2014). However, most studies focused on *Emiliana huxleyi*, which is one of the most widely distributed and dominated coccolithophore species (Zhai et al., 2013). Despite the overall significant and positive effect size, primarily contributed by *Emiliana huxleyi*, the other coccolithophore species included in this study - *Coccolithus braarudii* (n = 1), *Gephyrocapsa oceanica* (n = 1) and *Gephyrocapsa ericsonii* (n = 1) - exhibited negative responses. In contrast, *Coccolithus pelagicus* (n = 2) showed positive responses. This suggests the presence of potential species-specific responses in coccolithophores (Daniels et al., 2014; Frada et al., 2022; Gerecht et al., 2014; Rhodes et al., 1995). However, it's important to note that the sample size for these species is too small to draw definitive conclusions.

Warming significantly enhanced coccolithophore photosynthesis, indicating their adaptability to warmer conditions. However, the warming effect on photosynthesis was weaker compared to growth, suggesting a relatively stronger impact on respiration, as observed by Lopez-Urrutia et al. (2006). Additionally, this study did not find a statistically significant warming effect on coccolithophore calcification, suggesting a minor influence on their biomineralization. This result is in line with the portion of the meta-analysis by Harvey et al. (2013) related to coccolithophores. It is worth noting that the meta-analysis by Sheward et al. (2023) indicates that warming leads to a reduction in intracellular PIC and POC in *Emiliana huxleyi*. However, our analysis focuses on the photosynthesis and calcification rates of coccolithophores, which are distinct metrics from those in Sheward et al.'s study. For the majority of our data, both photosynthesis and calcification rates are scaled by the factor  $\mu$ , potentially suggesting that under faster growth rates, the accumulation of substances within the cell may not keep pace with cell division and proliferation. Furthermore, Sheward et al.'s research exclusively centers on *Emiliana huxleyi*, whereas our study includes other species. The sensitivity of photosynthesis and calcification in coccolithophores to temperature varies and may be related to species differences. In terms of the temperature effect on photosynthesis, it is relatively clear that within the optimal growth temperature range, as temperature gradually increases, photosynthesis becomes more sensitive to warming (Toseland et al., 2013). However, concerning calcification rates, there is no consistent trend in their sensitivity to warming (Feng et al., 2008; Langer et al., 2007; Zhang et al., 2020). This is likely due to variations in the optimal temperature ranges among different species (Sett et al., 2014).

The differential responses between different physiological processes are related to the intracellular resource allocation of coccolithophores. Under low temperature condition, cells prioritize resource allocation to biosynthesis, specifically rRNA production, to sustain growth and reproduction. With warming, resource allocation shifts towards photosynthesis (Toseland et al., 2013). The temperature range of warming



**Fig. 8.** The effects sizes of warming on diatoms of different size classes: (a) Growth; (b) Photosynthesis; (c) BSi:C. Numbers in parentheses indicate the number of experiments for calculation. The black horizontal solid line indicates the overall effect size of diatoms for the corresponding index. The black dashed lines indicate the confidence interval of the specific effect size. The red solid line indicates the zero level (no effect). An asterisk (\*) indicates a significant response.

(3–5 °C) set projected for the end of this century is likely not sufficient to reach the level at which resources are extensively allocated to photosynthetic rates. For many phytoplankton species, including *Emiliania huxleyi*, the growth rates continue to increase within a temperature range exceeding the maximum isolation temperature by 5–10 °C (Conte et al., 1998; Glé et al., 2008). Therefore, cell growth and reproduction are more sensitive to warming than photosynthesis. The unique physiological process of coccolithophores, calcification, is also influenced by temperature. Calcification is the process of intracellular accumulation of inorganic carbon. However, its response to warming is less pronounced compared to growth and photosynthesis. The optimal temperature for calcification is reported to be potentially lower than that for photosynthesis (Langer et al., 2007). However, studies by Sett et al. (2014) have found that with increasing temperature, coccolithophore cells also face a “reallocation” issue in terms of inorganic and organic carbon synthesis. When the temperature is slightly above the annual average temperature of their habitat (+5 °C), the increase in photosynthetic rate with temperature rise far exceeds the rate of calcification. Nonetheless, at temperatures significantly higher than the annual average (+10 °C), photosynthetic rate is inhibited while calcification rate continues to be promoted (Sett et al., 2014). In summary, within the chosen temperature range of this study, the general trend is that growth is maximally promoted, followed by photosynthesis, and finally, calcification.

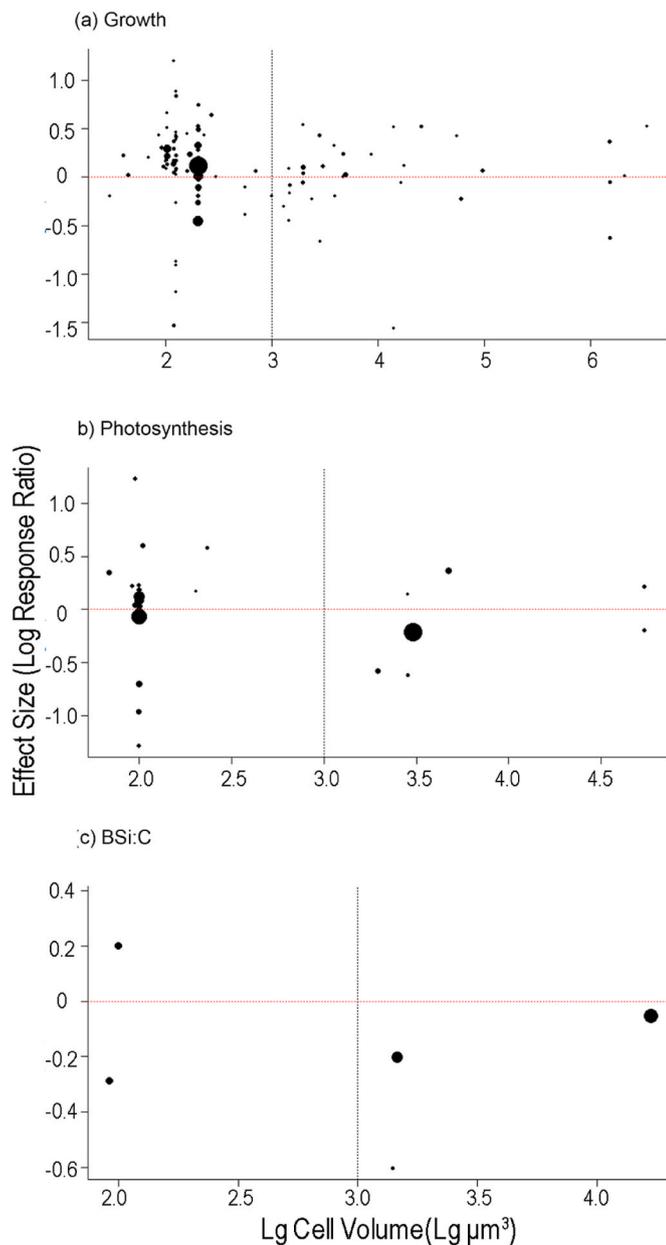
When photosynthesis exceeds calcification, the POC production is higher than that of PIC, leading to a lower PIC:POC ratio. Overall, this study, however, found that the impact of warming on the PIC:POC ratio of coccolithophores is not significant. While some experimental studies suggest that increasing temperature decreased the PIC:POC ratio in coccolithophore cells (Gerecht et al., 2014; Rosas-Navarro et al., 2016; Schlüter et al., 2014), there are also several experimental studies that find no significant effect of temperature on PIC:POC ratio (Feng et al., 2008; Fiorini et al., 2011; Johnson et al., 2022). The meta-analysis by Sheward et al. (2023) and Krumhardt et al. (2017) also yielded similar results. The PIC:POC ratio in coccolithophore cells is associated with cell density, which, in turn, affects the sinking rate of coccolithophores and their PIC:POC ratio (Milner et al., 2016). A decrease in the PIC:POC ratio may result in a lower sinking rate, subsequently impacting carbon export (Findlay et al., 2011). However, it is important to consider that factors influencing sinking rate are complex, and there is ongoing debate regarding the effect of temperature on the PIC:POC ratio. Therefore, it is

difficult to draw a broad conclusion regarding the impact of warming on PIC:POC ratio.

#### 4.1.2. Latitudinal variability

The observation suggests that coccolithophore growth and photosynthesis in the southern hemisphere may be more sensitive to rising temperatures. The growth rate results closely align with simulations conducted by Krumhardt et al. (2017). Furthermore, this finding is indirectly supported by satellite data, which indicates that coccolithophore bloom areas in the southern hemisphere have been more than twice as extensive as those in the Northern Hemisphere in recent years, coinciding with the warming trend (Moore et al., 2012).

The majority of observations (Fig. 5) are located in the 30–60°S and 30–60°N latitude range. Given the limited sample sizes (9 out of 37 total observations) in both low and high latitudes, along with the potential differences between laboratory and field culture temperatures, we focused on strains exposed to experimental temperatures that closely resembled those found in tropical and cold-zone environments (Bulgin et al., 2020). The effects observed in three cold-zone low-temperature (9–15 °C) experiments are greater than the overall effect, suggesting that the promotion effect of warming on the growth of coccolithophores in cold zones is stronger (Daniels et al., 2014; Langer et al., 2009) (Appendix A). In two tropical observations (23–25 °C), the growth of *Emiliania huxleyi* was still promoted by warming, while the growth of *Gephyrocapsa ericsonii* was suppressed (Frada et al., 2022). This suggests that under warming conditions, *Emiliania huxleyi* in tropical regions may still maintain a higher growth rate, but other species may not have the same advantage. Nevertheless, the increase in temperature results in a significant decreasing trend of PIC:POC in the southern mid-latitude regions (Fig. 4d), indicating the possible existence of differences between the northern and southern latitudes. However, the study by Krumhardt et al. (2017) suggest that warming has little to no significant impact on PIC:POC in mid-latitude regions. The reason may be due to the relatively narrow warming range (2–3 °C) of their study. Meanwhile, it is important to note that the sample size from this region in our study is relatively small ( $n = 4$ ), and further studies with a larger sample size are needed to confirm these findings. Therefore, based on the available information, the following conclusion can be drawn: The growth of coccolithophores in mid-latitude regions is significantly promoted by warming, and it appears that the cold-zone strains might also exhibit



**Fig. 9.** The log response ratio of: (a) growth; (b) photosynthesis; (c) BSi:C to warming on diatoms as a function of Lg (Base-10 logarithm) cell size. The radius of each circle corresponds to the weight (inverse of variance) of the respective data point. The red dashed line indicates no effect. The vertical dashed line serves as the boundary between 'large' and 'small' cells, representing  $1000 \mu\text{m}^3$ .

similar stimulation. There may be interspecies differences in the response of tropical strains to warming. Besides, there may be differences between the response of strains from the northern and southern latitudes. Growth of southern-latitude temperate strains may be more responsive to warming, but the PIC:POC ratio is likely to decrease.

Although coccolithophore blooms have been observed to occur on a larger scale in mid-latitude regions, with higher total biomass compared to other areas, it is indeed true that coccolithophores are also distributed in low-latitude and high-latitude regions (O'Brien et al., 2012; Winter et al., 2014). Due to the limitations of our analysis, which is based solely on published literature, a more comprehensive understanding of the latitudinal characteristics would require future research that includes a broader range of geographical areas and a greater diversity of coccolithophore species.

## 4.2. Diatoms

### 4.2.1. Growth, photosynthesis and biomineralization of diatoms

The growth rate of diatoms exhibited a significant increase in response to temperature rise. This result aligns with the meta-analysis conducted by Velthuis et al. (2022). This result also closely aligns with the meta-analysis conducted by Brandenburg et al. (2019). However, it is worth noting that their analysis includes a smaller number of diatom species (4 species) in relation to temperature, which could potentially result in one of their temperature-related growth analyses not showing statistical significance. However, it was not the case for photosynthesis. The impact of warming on diatom photosynthesis is not significant. It is noteworthy that both the mean effect sizes for growth rate and photosynthesis rate of diatoms were smaller compared to coccolithophores.

The difference in cell sizes between coccolithophores and diatoms could contribute to the disparities in their growth responses to temperature changes. A significant proportion (~71%) of coccolithophore cell diameters are less than  $10 \mu\text{m}$ , while the cell volume of *Emiliania huxleyi*, which comprises the majority of observations in this study, is approximately  $65 \mu\text{m}^3$  (Villiot et al., 2021). In this study, diatom cell volume exhibited a broad range, spanning  $\sim 30 \mu\text{m}^3$  to  $\sim 3\,400\,000 \mu\text{m}^3$ . Furthermore, a significant majority of diatom cells, accounting for 93.45% of the samples, had a cell volume exceeding  $100 \mu\text{m}^3$ . While it is possible for the growth rate of algae to exhibit a positive correlation with cell size when the cell volume is less than  $10 \mu\text{m}^3$  (Marañón, 2015), in this study, the selected algal cells had sizes predominantly exceeding  $50 \mu\text{m}^3$ . Therefore, based on the scope of this study, it can be inferred that the growth rate of the algae investigated is negatively correlated with cell size (Marañón, 2015). One possible reason for this could be that an increase in cell size reduces the surface-to-volume ratio, which hinders the transport of materials within the cell and consequently lowers the metabolic rate (Raven, 1998). Therefore, under the premise that warming increases the growth rate, larger-sized diatoms experience a smaller enhancement in growth compared to smaller-sized coccolithophores.

Furthermore, considering the overall effect size, it appears that diatom photosynthesis is not significantly stimulated by warming. This could be attributed to the larger average size of diatoms, which results in a greater packaging effect (Finkel, 2001). Packaging effect is one of the important factors influencing the photosynthetic efficiency of phytoplankton. It refers to the discrepancy in light absorption capacity between photosynthetic pigments within phytoplankton cells and those in the dissolved state (Morel and Bricaud, 1981). The packaging effect index ( $Q_a^*(\lambda)$ ) can be quantified as the ratio between in situ absorption coefficient ( $a_{ph}(\lambda)$ ) to the absorption coefficient of the dissolved state ( $a_{ph.sol}(\lambda)$ ), expressed as  $Q_a^*(\lambda) = a_{ph}(\lambda)/a_{ph.sol}(\lambda)$  (Huan et al., 2022). The smaller the diameter of phytoplankton cells, the closer they are to the wavelength range of photosynthetically active radiation (400–700 nm), resulting in a decrease in the packaging effect (Raven, 1998). Due to the smaller packaging effect, smaller cells are able to collect light more efficiently (Yun et al., 2010). The reduced light utilization efficiency in larger cells results in a more noticeable inhibition of their photosynthetic rate in terms of volume increase compared to the growth rate. In a study of unicellular algae, the size-scaling exponents for photosynthesis rates are lower than the commonly found  $-1/4$  exponent in heterotrophic organisms, while the size-scaling exponents for growth rates do not significantly differ from the  $-1/4$  exponent (Finkel, 2001). This difference leads to a weaker promotion of photosynthesis in larger diatom cells due to warming. Moreover, taking into consideration the resource allocation issue (Toseland et al., 2013), which states that under small temperature increases (with a difference of less than  $10 \text{ }^\circ\text{C}$  from the habitat temperature), cells are more likely to prioritize growth and reproduction over photosynthesis adaptation, it is not difficult to understand the relatively modest enhancement of photosynthesis in

diatoms under warming.

The process of silicification is a unique physiological feature of diatoms (Pancić et al., 2019), but the impact of warming on this process is not significant. Based on the mean effect values, our study provides evidence that warming leads to decrease in BSi:C. High temperatures can weaken the silicification process of diatoms, particularly when the optimal growth temperature is exceeded. For instance, a temperature increase of 5–10 °C above the optimum has been shown to cause a decrease in biogenic silica (Kuefner et al., 2020; Sheehan et al., 2020). However, due to the narrow range of temperature increase selected in this study (3–5 °C), this effect may not be significant. Meanwhile, it is reported that the silicification of diatom cell walls and the transport of silicic acid are closely coupled with the cell cycle, resulting in the degree of silicification being dependent on the growth rate (Martin-Jézéquel et al., 2000). This implies that the silicification process in diatoms is regulated by growth, and according to the resource allocation theory, cells prioritize resource allocation for growth and reproduction.

On the other hand, the cellular BSi:C ratio is also influenced by the accumulation of POC, primarily through the process of photosynthesis. However, the regulatory pathways of photosynthesis and silicification are not closely interconnected (Martin-Jézéquel et al., 2000). However, this does not imply that photosynthesis and silicification are unrelated, as there is a relationship between light intensity and the half-saturation constant for silicon uptake in diatoms, which differs between centric and pennate diatoms (Shi et al., 2015). However, there is no clear evidence indicating that silicification can directly regulate the growth and reproduction of diatoms. Therefore, considering the sequence of resource allocation (Toseland et al., 2013), the effects of warming on the BSi:C ratio was smaller and less significant than those on growth and photosynthesis.

Additionally, our meta-analysis included a wide range of diatom species, leading to the overlapping of species-specific responses. Different diatom species may respond differently to warming, and their adaptive mechanisms may vary. For example, although this study primarily emphasizes the relative disadvantage of diatoms as a functional group in response to warming, certain diatom species may have evolved specific adaptive mechanisms to enhance their tolerance to warming conditions. A recently published paper has revealed that the diatoms *Chaetoceros curvisetus/pseudocurvisetus*, through adjustments in cellular lipids and other means, exhibits enhanced adaptability to elevated temperatures (Vrana et al., 2023). Therefore, in future research, it would be beneficial to conduct detailed studies on certain diatom species to obtain more targeted results.

#### 4.2.2. Latitudinal variability

The latitudinal variation characteristics of diatoms are more significant compared to coccolithophores, due to a wider distribution of data across latitudes. However, data from low-latitude regions in the Southern Hemisphere are still lacking in our study. Regarding the growth rate, the species isolated from higher latitudes, particularly the Southern Hemisphere, exhibit a more pronounced response to warming, with enhanced growth rates (Figs. 6a and 7a).

The growth of diatoms isolated from the high-latitude regions were promoted to a larger extent, as a consequence of the narrow temperature range for the thermal response curves of the growth of these species (Chen, 2015). The 3–5 °C of temperature increase, which was applied as the criteria in this study, would bring the temperature closer to the optimal growth temperature for high-latitude diatoms compared to those in mid and low-latitude regions. According to the Eppley-Norberg curve, the growth rate increases more rapidly as the temperature approaches the optimum temperature (Grimaud et al., 2017; Norberg, 2004).

Due to the non-significant effects of BSi:C observed across different latitudes, and considering the small sample size, it is difficult to infer the relationship between BSi:C response and latitude. However, considering the lower average effect values in latitude regions, there is a possibility

that the silica deposition in high-latitude diatoms is inhibited by warming. It is still important to note that the maximum growth thermal threshold (5–6 °C) of polar diatoms is significantly lower compared to diatoms in mid- and low latitudes (Coello-Camba and Agusti, 2017).

#### 4.2.3. The role of diatom size

Recent studies have shown that the size of diatom cells may be related to competitive advantages within diatom species and with other algal species (Ando and Katano, 2018; Terseleer et al., 2014; Zhang and Luo, 2022). Therefore, it was necessary to consider diatom cell size.

Our results indicate that smaller diatoms exhibited faster growth and a higher photosynthetic rate compared to larger diatoms under warming. In other words, there was an inverse relationship between diatom size and growth rate in response to temperature elevation. This indicates that small-sized diatoms are more competitive than large-sized diatoms under warming conditions. Similarly, previous studies have reported that warming conditions not only result in a reduction in cell size within the same diatom species but also lead to a shift towards a smaller size distribution in diatom communities (Montagnes and Franklin, 2001; Svensson et al., 2014).

The growth advantage of small cells primarily arises from their larger surface area-to-volume ratio, allowing them to efficiently acquire nutrients due to reduced diffusion boundary layers and lower nutrient flux per unit membrane area required for maximum specific growth rate (Zaoli et al., 2019). Additionally, small cells benefit in photosynthesis from easier carbon dioxide diffusion to the photosynthetic core (Huan et al., 2022; Raven, 1998). They can meet their catalytic needs with fewer ribulose-1,5-bisphosphate carboxylase-oxygenase enzymes, which are costly to synthesize in terms of energy, carbon, and nitrogen (Raven, 1998). Consequently, small cells have lower photosynthetic costs compared to larger cells. Given these characteristics, it is reasonable to anticipate that under the small-scale temperature increases considered in this study, smaller diatoms exhibit stronger cellular responses in terms of growth and photosynthesis.

Given the vital role of growth and photosynthesis in the survival of diatom species compared to silicification, our findings suggest that smaller diatoms may have a competitive advantage in warmer temperatures. Nevertheless, in oceanic environments, various factors, such as grazing pressure (Charalampous et al., 2021) and changes in silicate concentrations (Martin-Jézéquel et al., 2000), can influence the competition among diatom species. Thus, comprehensive analyses considering multiple factors remain essential for a more accurate projection.

#### 4.3. Coexistence and competition between coccolithophores and diatoms

Our results demonstrate that coccolithophores exhibit a more pronounced positive response in terms of growth and photosynthesis in a warmer condition. This implies that warming may cause a stronger advantage for coccolithophores over diatoms. Similarly, long term observation has revealed an increase in the field abundance of coccolithophores from 1990 to 2014 in the subtropical North Atlantic (Krumhardt et al., 2016). With the smaller size, coccolithophores exhibit distinct nutrient uptake mechanisms compared to diatoms. Previous studies have indicated that coccolithophore *Emiliania huxleyi* shows greater activity in xanthophyll cycle pigment accumulation and the transformation from diadinoxanthin to diatoxanthin, particularly under nutrient limitation, compared to diatom *Phaeodactylum tricorutum* (Zhao et al., 2015). This suggests that coccolithophores may employ different resource and energy allocation mechanisms than diatoms, potentially accounting for the divergent responses to warming observed between these two groups.

Meanwhile, the results of this study align closely with meta-analysis by Seifert et al. (2020), both emphasizing the advantage of coccolithophores under warming conditions. While Seifert et al. (2020) compared coccolithophores to all functional groups, our study specifically

compared coccolithophores to diatoms, highlighting the relative advantage of coccolithophores over diatoms under warming conditions.

On the other hand, a warmer ocean situation may result in a shallower mixed layer depth in a large range of the global ocean, as indicated by field observation data and model simulation results (Ando and McPhaden, 1997; Chen and Wang, 2015; Lakshmi et al., 2009; Yeh et al., 2009). A shallower mixed layer depth is associated with a decreased concentration of effective nutrients in the euphotic zone (Diehl, 2002; Klausmeier and Litchman, 2001). This would put diatoms at a greater disadvantage in competing with coccolithophores in a warming ocean (Cermeno et al., 2011; Lampe et al., 2021). While rising temperatures have been associated with more frequent algal blooms in recent years, a further increase in temperature beyond current levels could lead to less frequent occurrences of diatom blooms. The global diatom abundance is currently decreasing (Costa et al., 2021), indicating that diatoms as a phytoplankton functional group are potentially at risk.

For coccolithophores, their distribution has been shifting towards polar regions in recent years, and the gradually rising sea temperature is one of the key factors driving this poleward expansion (Mohan et al., 2008; Rigual Hernandez et al., 2020; Thomas et al., 2012; Winter et al., 2014). The increase in temperature provides the opportunity for coccolithophores to occupy ecological niches in polar regions. For diatoms, the positive effects of warming are stronger in high latitude regions, particularly in southern high latitudes. However, polar diatoms face challenges from the expansion of other species, such as coccolithophores. This is likely to cause changes in the population structure of phytoplankton and pose new challenges for the survival of diatoms. Observations and model simulations have already reported a decreasing trend in global diatoms abundance (Rousseaux and Gregg, 2015; Seifert et al., 2023). Based on the above information, a conceptual diagram depicting the response of coccolithophores and diatoms to warming has been created (Fig. 10).

This study examines the impact of warming from a specialized perspective. In future analyses, ocean acidification, nutrient concentration, and light intensity could be considered as factors influencing competition among algae. These factors also have a significant impact on the competition between coccolithophores and diatoms. In light of both this study and published literature, it is evident that increased  $pCO_2$  levels have a negative effect on coccolithophore growth and calcification rates (J. Meyer & U. Riebesell, 2015; Seifert et al., 2020; Harvey et al., 2013; Sheward et al., 2023). This has the potential to reduce the

competitive advantage of coccolithophores in response to warming. Conversely, elevated  $pCO_2$  levels may enhance diatom growth, although their effect size is smaller than that of warming (Seifert et al., 2020; Velthuis et al., 2022; Bach and Taucher, 2019). Furthermore, a shallower mixed layer depth in the future is expected to reduce average nutrient concentrations, significantly affecting diatoms growth due to their higher nutrient sensitivity (Seifert et al., 2020). Consequently, the dynamics of coccolithophore-diatom competition in the future are likely to be intricate. However, there are also studies simulating the outcomes of competition under future multi-factor changes in the ocean. Even though coccolithophores exhibit a negative response to acidification, these simulations tend to favor coccolithophores as the “winners”, while diatoms face a greater risk of survival, especially in polar regions (Boyd et al., 2015; Henson et al., 2021; Liu et al., 2022; Seifert et al., 2023). Our study can serve as the foundation and starting point for future related research.

Moreover, it is important to note that the coccolithophore data collected in this study primarily pertains to mid-latitude regions, with limited representation from other latitudes. Additionally, a significant portion (over 80%) of the studies included in this research focuses on a single species, *Emiliania huxleyi*, to the neglect of other coccolithophore species. Relatively speaking, the diversity and distribution of diatom species in the data are much broader. Therefore, to gain a deeper understanding of the response of the entire coccolithophore functional group to climate change, further research on coccolithophore species other than *Emiliania huxleyi* will be necessary. Furthermore, there is a lack of available current research on diatom species from low-latitudinal regions in the Southern Hemisphere. Therefore, future studies should consider expanding their geographical coverage.

### 5. Conclusion

In conclusion, our analysis reveals that warming has significant positive effects on the growth and photosynthesis of coccolithophores; while for diatoms, the positive effect of warming is significant only for growth. And the overall effects on coccolithophores were larger than those on diatoms, indicating that coccolithophores have a greater advantage over diatoms under warming conditions. The effects of warming on biomineralization of both groups were non-significant. Our results suggest that under the projected warming for the end of this century, cellular resource allocation enhances enzymatic reactions in

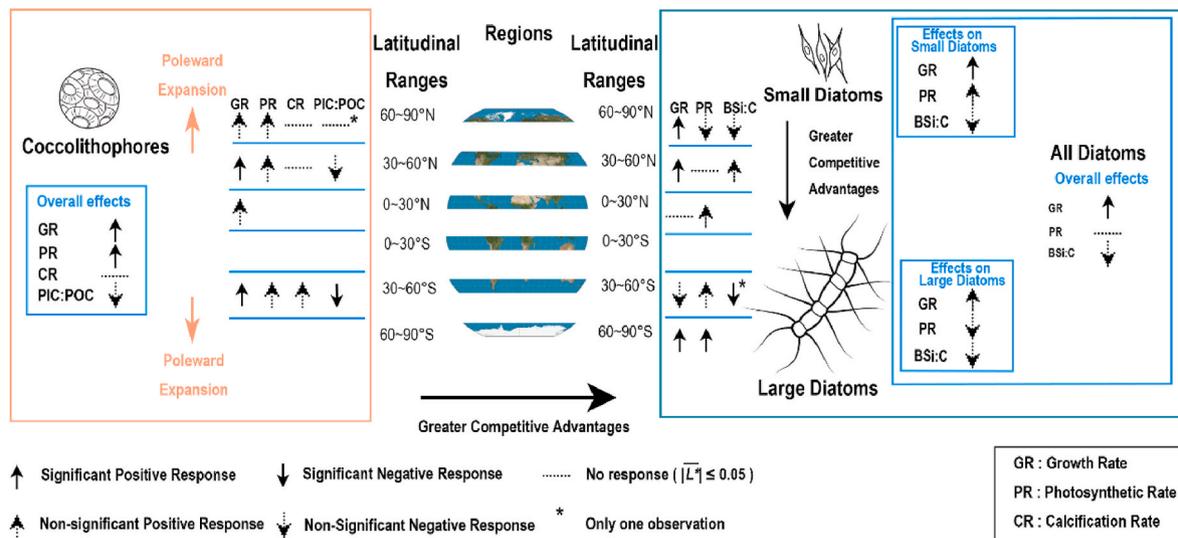


Fig. 10. Conceptual illustration highlighting the varied responses of diatoms and coccolithophores in a warmer scenario, along with the broader implications derived from the study. Please acknowledge that the distribution of data across latitudinal regions is not uniform, resulting in data gaps in certain latitudinal groups (The images of coccolithophores and diatoms were sourced from: Ask A Biologist coloring page: askabiologist.asu.edu/activities/coloring).

the order of growth, photosynthesis, and biomineralization. High-latitude diatoms and coccolithophores exhibit a relatively more pronounced response to warming, especially in the Southern Hemisphere. Furthermore, warming enhances the competitive advantage of small-sized diatoms over the large ones. Future research should encompass a broader range of phytoplankton species and geographic locations to obtain a more comprehensive view.

### Author statement

**Jiawei Wang (First Author):** Conceptualization, Methodology, Software, Investigation, Formal Analysis, Writing - Original Draft;  
**Cong Zeng:** Methodology; Validation; Writing - Review & Editing.  
**Yuanyuan Feng:** Conceptualization, Funding Acquisition, Resources, Supervision, Writing - Review & Editing.

### Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

### Data availability

The data that support the findings of this study are available in the supporting information of this article.

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### Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.marenvres.2023.106275>.

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