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Elemental stoichiometry of the key calcifying marine phytoplankton *Emiliania huxleyi* under ocean climate change: A meta-analysis

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Abstract

The elemental composition of marine microorganisms (their C:N:P ratio, or stoichiometry) is central to understanding the biotic and biogeochemical processes underlying key marine ecosystem functions. Phytoplankton C:N:P is species specific and flexible to changing environmental conditions. However, bulk or fixed phytoplankton stoichiometry is usually assumed in biogeochemical and ecological models because more realistic, environmentally responsive C:N:P ratios have yet to be defined for key functional groups. Here, a comprehensive meta-analysis of experimental laboratory data reveals the variable C:N:P stoichiometry of *Emiliania huxleyi*, a globally significant calcifying phytoplankton species. Mean C:N:P of *E. huxleyi* is 124C:16N:1P under control conditions (i.e. growth not limited by one or more environmental stressors) and shows a range of responses to changes in nutrient and light availability, temperature and pCO$_2$. Macronutrient limitation caused strong shifts in stoichiometry, increasing N:P and C:P under P deficiency (by 305% and 493% respectively) and doubling C:N under N deficiency. Responses to light, temperature and pCO$_2$ were mixed but typically shifted cellular elemental content and C:N:P stoichiometry by ca. 30% or less. Besides these independent effects, the interactive effects of multiple environmental changes on *E. huxleyi* stoichiometry under future ocean conditions could be additive, synergistic or antagonistic. To synthesise our meta-analysis results, we explored how the cellular elemental content and C:N:P stoichiometry of *E. huxleyi* may respond to two hypothetical future ocean scenarios (increased temperature, irradiance and pCO$_2$ combined with either N deficiency or P deficiency) if an additive effect is assumed. Both future scenarios indicate decreased calcification (which is predominantly sensitive to elevated pCO$_2$), increased C:N, and up to fourfold shifts in C:P and N:P. Our results strongly suggest that climate change will significantly alter the role of *E. huxleyi* (and potentially other calcifying phytoplankton species) in marine biogeochemical processes.

KEYWORDS
C:N:P, calcification, climate change, coccolithophore, elemental composition, phytoplankton, PIC:POC, Redfield

1 | INTRODUCTION

Predicting the response of marine microorganisms to our changing climate is a major challenge facing marine scientists. Marine environments are expected to experience altered temperature, light and chemical regimes (Fox-Kemper et al., 2021) that will influence core ecosystem functions (Bindoff et al., 2019; Cooley et al., 2022). The impacts of climate change, particularly ocean acidification, on the physiology of marine organisms has been studied for representatives of many groups (e.g. see meta-analyses by Kroeker et al., 2013, Wittmann & Pörtner, 2013 and references therein). Less well characterised are how physiological responses to ocean climate change may drive shifts in elemental stoichiometry (organism carbon, nitrogen and phosphorus content and their respective elemental ratios). C:N:P stoichiometry connects organism metabolic requirements with nutrient supply and turnover, providing a biochemical link between the environment and ecology (Falkowski et al., 1998; Moreno & Martiny, 2018; Sterner & Elser, 2002) that influences broader ecosystem functions, including primary productivity, nutrient cycles, trophic structure and energy fluxes and carbon export (Welti et al., 2017). Marine microorganisms have some capacity for flexibility in their cellular C:N:P stoichiometry, which may influence the tolerance level of each species towards changing ocean conditions (Martiny et al., 2022). As such, understanding species-specific flexibility in cellular elemental composition under changing conditions is at the heart of understanding and predicting the impacts of climate change on marine phytoplankton communities, biogeochemical processes and ecosystem functions.

Observations show that particulate C:P, N:P and C:N in seawater are spatially variable, differing latitudinally and between oligotrophic gyres and high-latitude or equatorial upwelling regions (DeVries & Deutsch, 2014; Martiny et al., 2013; Tanioka et al., 2022; Weber & Deutsch, 2010). Explanations for this spatial heterogeneity include the varied composition of phytoplankton communities in different marine biomes (Mills & Arrigo, 2010; Weber & Deutsch, 2012), as phytoplankton stoichiometry is variable at the organism level (Finkel et al., 2016; Garcia et al., 2018; Quigg et al., 2003) and responds to environmental perturbations (Garcia et al., 2018; Geider & La Roche, 2002). For example, the relatively low 11N:1P of cold-water diatoms may contribute to lower particulate N:P in the Southern Ocean where they dominate communities (Weber & Deutsch, 2010, 2012). Despite the observational and experimental evidence for variable phytoplankton stoichiometry, many biogeochemical and ecological models addressing the effects of climate change on global marine ecosystems assume a fixed elemental stoichiometry for marine plankton known as the 'Redfield ratio' (106C:16N:1P) (Redfield, 1958). Several newer-generation models now incorporate some level of variable phytoplankton stoichiometry (typically variable C:P while C:N remains fixed, e.g. Galbraith et al., 2015; Hayashida et al., 2019; Kwon et al., 2022; Séférian et al., 2020). The implementation of variable stoichiometry tends to improve model representation of observed regional patterns in particulate C:N:P (Inomura et al., 2022; Kwon et al., 2022; Moreno et al., 2018) and modelled patterns and trends in net primary productivity tend to

better match the contributions of phytoplankton to global carbon fluxes expected from observational data (Galbraith & Martiny, 2015; Kwiatkowski et al., 2018). However, the ultimate influence of variable phytoplankton C:N:P on marine net primary productivity, export productivity or oceanic CO_2 uptake remains uncertain (Kwon et al., 2022). Implementing variable C:N:P stoichiometry within next-generation marine biogeochemical and ecological models (Inomura et al., 2022; Kwiatkowski et al., 2018; Matsumoto et al., 2020) remains constrained by available source data for both fixed and flexible phytoplankton C:N:P, which are typically derived from small numbers of experiments performed on only a few genetic strains (Moreno & Martiny, 2018). One approach to address this shortcoming is to use systematic meta-analysis methods to analyse the pooled effect of individual environmental changes on the C:N:P stoichiometry of important marine plankton groups that have a large, existing amount of experimental research into their physiology.

The flexible C:N:P stoichiometry of the 'calcifying phytoplankton', the coccolithophores, is of particular interest as they are regarded as the most productive calcifying organisms on Earth with a unique role in ocean carbon fluxes (Rost & Riebesell, 2004). The coccolithophore species *Emiliania huxleyi* is unquestionably the most well-studied of the >200 species of extant coccolithophores and arguably one of the most well-studied of all microorganisms. Its virtually global biogeographic distribution is testament to its tolerance for an extremely broad range of environmental regimes and it is notable for forming expansive temperate and subpolar blooms (Tyrrell & Merico, 2004) that can contribute up to 40% of local primary production (Poulton et al., 2013). *E. huxleyi* is a prolific producer of calcium carbonate; and therefore contributes simultaneously to both the biological carbon pump and the carbonate counter pump, the balance between which impacts surface-air CO_2 fluxes and contributes substantially to carbon export into the deep ocean (Rost & Riebesell, 2004; Westbroek et al., 1993). The global ecological and biogeochemical importance of *E. huxleyi* alongside the large quantity of available data on its physiology and biology justifies its use as a representative for calcifying phytoplankton in Earth system models that resolve phytoplankton functional types with distinct biogeochemical roles (Follows et al., 2007; Follows & Dutkiewicz, 2011).

Existing reviews of the physiology and biogeochemical characteristics of *E. huxleyi* (Fielding, 2014; Findlay et al., 2011; Krumhardt et al., 2017; Meyer & Riebesell, 2015; Paasche, 2001; Rost et al., 2002; Zondervan, 2007) have predominantly addressed variability in cell carbonate (PIC) and organic carbon (C) content, especially under perturbated carbonate chemistry. The scope of these reviews either performed a qualitative rather than quantitative review, did not follow a systematic and reproducible meta-analysis methodology, or have not considered a broader range of environmental variables and/or the impact of one or more environmental perturbations on stoichiometric parameters other than PIC and C.

Here, our aim is to quantify the impact of environmental change on the elemental content (PIC, C, nitrogen N and phosphorus P) and stoichiometry (C:N:P and PIC:C) of *E. huxleyi* through a synthesis and meta-analysis of published data from laboratory

studies. Our specific objectives are to (1) calculate 'mean' values for *E. huxleyi* cellular elemental content and stoichiometric ratios when cultured under control conditions (i.e. no temperature, irradiance, pCO_2 or nutrient stress), (2) calculate the direction and magnitude of response (using an effect size metric, L^*) of cellular elemental content, C:N:P stoichiometry and PIC:C in response to four categories of environmental stressors that are relevant for future global ocean change: temperature, light availability, pCO_2 concentrations and nutrient limitation, and (3) estimate the overall response of *E. huxleyi* C:N:P stoichiometry to future changing ocean conditions using an additive approach applied to the calculated mean effect sizes derived for Objective 2.

2 | METHODS

2.1 | *Emiliania huxleyi* stoichiometry database

2.1.1 | Literature search and screening criteria

We searched the literature for publications where a strain of *E. huxleyi* was grown in a laboratory setting and cellular elemental content and/or other stoichiometric data were reported, with the aim of compiling a single database of *E. huxleyi* stoichiometry data and relevant ancillary information from which meta-analyses can be performed. The literature search terms prioritised the mention of organic and inorganic carbon content in publications, as these are the most routinely measured elemental constituents of coccolithophores. We conducted a full-text search on 2 February 2018 using Google Scholar and the search term "Emiliania huxleyi" AND "particulate organic carbon" OR "particulate inorganic carbon", yielding 2454 publications for suitability screening, of which the first 1000 are retrievable. We conducted a later search of ISI Web of Science (WoS) on 8 October 2021 (searching title, abstract, and keywords of the Core Collection Database) using the search string (TS=("Emiliania huxleyi")) AND (TS=experiment* OR TS=cultur*) AND (TS="organic carbon" OR TS="particulate inorganic carbon" OR TS=biomass OR TS=calcite OR TS=carbonate OR TS="PIC" OR TS="POC" OR TS="PIC:POC" OR TS="inorganic to organic carbon ratio"), which yielded a further 426 results published between 2018 and 2021 of which 159 (37%) were duplicate records of those present in the Google Scholar search. The 267 non-duplicate WoS search results were aggregated with those from the Google Scholar search for literature screening (Figure S1).

In total, the titles of all 1256 publications were screened for relevance based on whether it seemed plausible that the publication might report relevant raw data on *E. huxleyi* stoichiometry. For publications deemed potentially suitable for inclusion in the *Emiliania huxleyi* Stoichiometry Database (EhSD), the abstract and then full text of the manuscript was retrieved and examined to determine whether the reported data were suitable for data extraction. Publications were excluded at any stage of screening if (1) they did not report data from *E. huxleyi*, (2) they did not report elemental content (PIC, C, N, P) or stoichiometric (C:N, N:P, C:P or PIC:C) data in any form, (3) data

were not from a laboratory monoculture experiment of *E. huxleyi* but instead from mesocosm or mixed-assemblage microcosm experiments, in-situ plankton sampling, satellite or remote sensing, sediment trap or fossil material, (4) the publication did not report original raw data because it was a modelling study, review/compilation or a conference abstract, (5) the publication reported appropriate data that were already included from another source (avoiding pseudo-replication) or (6) data reported was for aggregates containing *E. huxleyi*, that is, non-cellular data were reported (see Supplementary Methods for further details of the screening process).

The screening of paper titles, abstracts and full text was performed manually by author R.M.S with particular attention to the reported methods, data tables and figures and supplementary information. Documentation of the systematic literature review is shown in Figure S1 and the full inclusion/exclusion justification for each publication screened at abstract or full text is reported in Table S1. Overall, 115 studies satisfied the inclusion criteria (Table S2) and were subject to data extraction.

2.1.2 | Data extraction

Data were extracted from publication tables where possible or from figures using ImageJ (v1.51t, https://imagej.nih.gov/ij/index.html). If necessary, the publication authors were contacted directly to request the original datasets. Data (mean, standard deviation or standard error of replicate cultures and number of replicate cultures) for growth rate, cellular content of PIC, C, N or P, production rates (e.g. C per cell per day), and/or PIC:C, C:N, N:P or C:P were recorded as unique observations for each strain and experimental treatment reported in each publication. Data for PIC, C, N or P were standardised to $pg\,cell^{-1}$ units and stoichiometric ratios to mol:mol units. In addition to stoichiometric data, relevant information on the *E. huxleyi* strain used, experimental conditions and methodological design were collected in the EhSD for each experimental observation. Further information on the data extraction methodology and which ancillary information was recorded can be found in the Supplementary Methods. The full list of publications from which stoichiometry data have been extracted for the EhSD is shown in Table S2. The *E. huxleyi* stoichiometry database (EhSD version 3, 1 February 2023; Sheward et al., 2023) is available as a Microsoft Excel sheet at Zenodo, doi: 10.5281/zenodo.7594880.

2.2 | Calculating the effect size of different environmental treatments

To assess the impact of environmental changes on *E. huxleyi* stoichiometry we statically evaluated the effect of marine environmental change ('treatments': changes in temperature, light, carbonate chemistry and macronutrient availability; see Table 1 and Supplementary Methods for further explanation of the definition of each environmental treatment) on nine cellular parameters (growth

TABLE 1 Summary of experimental environmental conditions that are defined as 'control' and 'treatment' for the purposes of this meta-analysis. Note that control and treatment definitions may differ from definitions in the original publication. Publications were assessed on a case-by-case basis (see Supplementary Methods and Tables S3–S6). Experiments categorised as 'controls' that were not experiencing 'treatment' conditions in any other environmental parameter were included in the analysis for Figure 1.

Environmental treatment category	'Control' definition[d]	'Treatment' category label	'Treatment' category definition[d]
Temperature	Experiment temperature at or within 3°C of the temperature in culture collection or at the isolation location.	+T (High temperature)	Temperature increase of 2°C or more applied to the treatment experiment relative to the control experiment.
Irradiance[a]	Daily photon flux (incorporating both irradiance level and daylength) is between 2.16 and 11.52 mol photons m^{-2} day^{-1}	−L (Low light)	Daily photon flux is <2.16 mol photons m^{-2} day^{-1}
		+L (High light)	Daily photon flux is >11.52 mol photons m^{-2} day^{-1}
Nutrient deficiency[b]	N:P ratio of initial media between 10 and 50	−N (nitrate deficiency)	N:P of initial media <10
		−P (phosphate deficiency)	N:P of initial media >50
Carbonate chemistry[c]	pCO_2 between 280 and 430 µatm (broad class for 'ambient' conditions used as control, as this was variable across studies from pre-industrial values to near-present-day values of ca. 400 µatm)	<280	<280 µatm (low/glacial CO_2 levels)
		430–580	>430–580 µatm (IPCC RCP 2.6, 490 ppm)
		580–720	>580–720 µatm (IPCC RCP 4.5, 650 ppm)
		+CO$_2$	>720–1000 µatm (IPCC RCP 6.0, 850 ppm)
		++CO$_2$	>1000–2000 µatm (IPCC RCP 8.5, 1370 ppm)
		>2000	>2000 µatm

[a]Choice of ambient light conditions is informed by range of maximum metabolic rates (Krumhardt et al., 2017).

[b]Nutrient deficiency is defined as a (chemical) stoichiometric lack of N relative to P or vice versa (Moore et al., 2013) and guided by the N:P biological stoichiometry of Redfield (1958) and the half-saturation constants for N and P in *E. huxleyi* (Krumhardt et al., 2017).

[c]pCO_2 treatment categories were guided by IPCC Representative Concentration Pathway (RCP) emission scenarios (van Vuuren et al., 2011) relative to present-day/pre-industrial 'control' concentrations.

[d]See Supplementary Methods for further explanation of the treatment levels chosen.

rate, elemental content of PIC, C, N and P, and stoichiometric ratios of (PIC:C, C:N, N:P and C:P) using mean weighted log-transformed response ratio (L^*) as our measure of effect size. A positive L^* value indicates that across all relevant observations, the environmental treatment led to an increase in the cellular parameter relative to the parameter under control conditions. Conversely, a negative L^* value indicates that across all observations the environmental treatment led to a decrease in the cellular parameter relative to the control.

For each cellular parameter and environmental category (Table 1), L^* was calculated from paired control-treatment observations contained in the EhSD. For example, the L^* calculation to quantify the effect of elevated pCO_2 on growth rate uses paired observations from all publications that report suitable growth rate data for a culture grown under ambient pCO_2 conditions (the control) and its paired culture grown under a defined concentration of elevated pCO_2 conditions (the treatment). L^* and its 95% confidence intervals (95% CI) are calculated based on Hedges et al. (1999) as follows:

$$L^* = \frac{\sum_{i=1}^{k} w_i^* \left(\ln(\overline{X}_T) - \ln(\overline{X}_C) \right)_i}{\sum_{i=1}^{k} w_i^*}$$

$$95\%\, CI = L^* \pm 1.96 \left(\sqrt{\frac{1}{\sum_{i=1}^{k} \frac{1}{w_i}}} \right)$$

where $\overline{X}_T$ and $\overline{X}_C$ are the mean value of cellular elemental content (pg cell^{-1}), stoichiometric ratio (mol:mol) or growth rate (day^{-1}) for the ith control (C)–treatment (T) observation pair, k is the total number of control–treatment pairs and w_i^* is a function of within-study variance and between-study variance (see Supplementary Methods). The effect of the environmental treatment on the cellular parameter in question was significant if the 95% CI of L^* did not overlap 0 and nonsignificant if the 95% CI of L^* did overlap 0. Full details of all L^* calculation steps are provided in the Supplementary Methods. To simplify discussion of the results, we back-calculated mean percentage change from L^* as percentage change = [100*(exp(L^*) − 1)].

For each L^* calculation, suitable control-treatment pairs (mean, standard deviation and number of replicate measurements for each cellular parameter) were identified by first shortlisting (from the complete list of publications shown in Table S2) publications that had undertaken experiments with the relevant environmental treatment. Next, the subset of experimental observations in the EhSD relating to those publications were screened to assess whether the data were suitable for inclusion in the L^* calculation. Data were deemed unsuitable for inclusion if (1) there was no 'control' or 'treatment' experiment as defined in Table 1; (2) the data of interest (growth rates, elemental content, stoichiometry) were reported for only 'control' or 'treatment' conditions but not for both; (3) 'treatment' data were
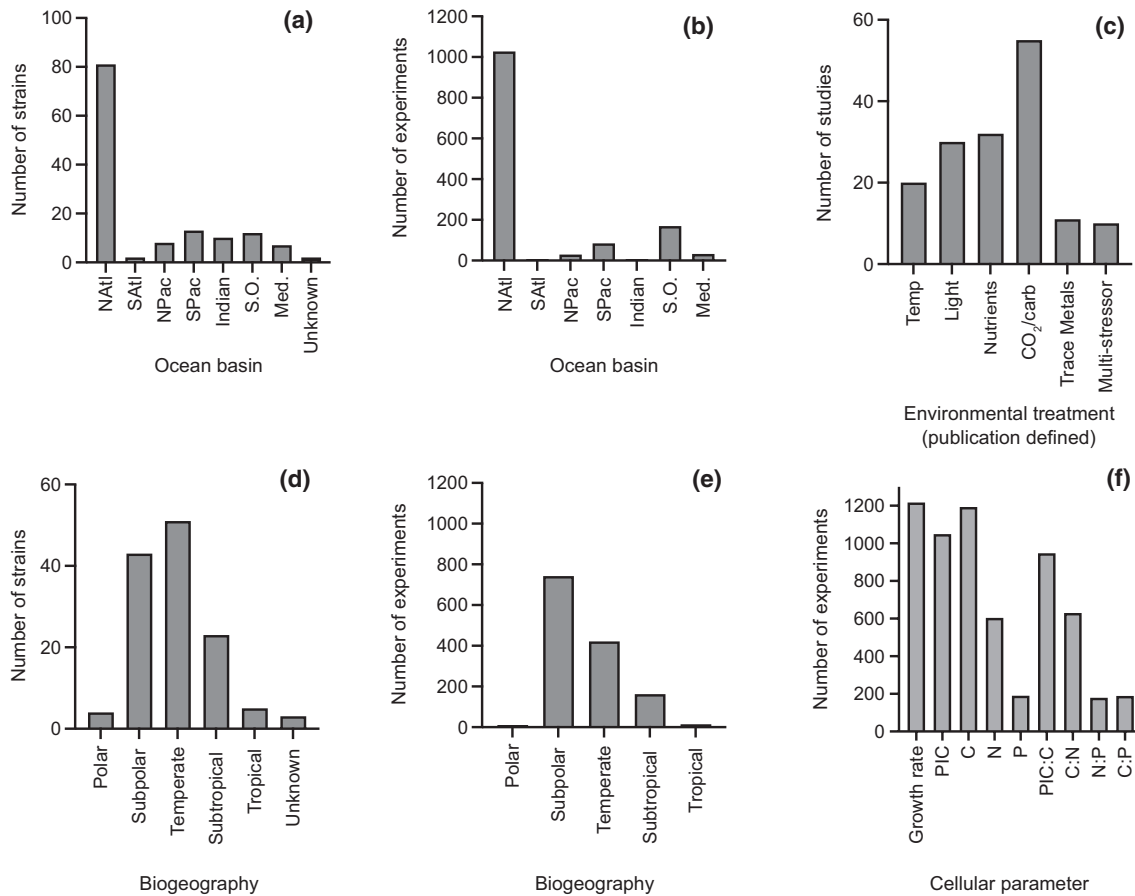
FIGURE 1 Overview of the *Emiliania huxleyi* Stoichiometry Database (EhSD) created and analysed in this meta-analysis. NAtl = North Atlantic Ocean, SAtl = South Atlantic Ocean; NPac = North Pacific Ocean; SPac = South Pacific Ocean; Indian = Indian Ocean; S.O. = Southern Ocean; Med. = Mediterranean Sea; and Unknown = latitude and longitude of strain isolation location were not given in study and could not be identified through other means.

obtained from an experiment where a second or third environmental variable was outside of control conditions as defined in Table 1 (constituting a multi-stressor experiment, e.g. a high temperature experiment was performed at elevated rather than ambient pCO$_2$ as defined in Table 1); (4) the publication reported insufficient information to determine the control and/or treatment conditions applied to one or more experiments (e.g. day length was not reported in a high light treatment paper); (5) experiments were performed using a non-calcified strain of *E. huxleyi*; or (6) data were collected during stationary phase as defined by the publication authors or as evident from data of cell density through time reported in the publication. A complete record of the publications shortlisted from the EhSD for each environmental L^* calculation and justification for the inclusion or exclusion of their associated experimental data in the calculation of L^* are detailed in Tables S3–S6. Lastly, the subset of suitable control–treatment pairs were assigned an environmental classification label following the category descriptions in Table 1, data with the same environmental classifications were aggregated, and L^* calculated for each cellular parameter using Microsoft Excel for Mac 2011. If more than one experiment in a publication was performed under control conditions (Table 1), a single experiment

was designated as the control for the purpose of this analysis (Supplementary Methods and Tables S3–S6).

2.3 | Mean *E. huxleyi* C:N:P under control conditions

To quantify the mean cellular elemental content (PIC, C, N, P) and mean stoichiometry (PIC:C, C:N, C:P and N:P) of *E. huxleyi* under control conditions, the full EhSD was filtered to exclude data from any experiments grown under conditions outside of control temperature, light, macronutrients or carbonate chemistry conditions or any other non-control environmental manipulation, for example, non-control trace metal (Fe, Cd, Zn etc.), data from non-calcified strains, and data reported as having been sampled during stationary growth phase. Statistical descriptors (mean, median, quartiles, range) were calculated using the 'descriptive statistics' function of GraphPad Prism (v8) and the resulting mean PIC, C, N and P were additionally used to calculate mean PIC:C, C:N, N:P and C:P ratios. Stoichiometric ratios were also calculated as the mean of all observation-specific PIC:C, C:N, N:P and C:P values.

2.4 | Response of *E. huxleyi* to future climate scenarios

To synthesise our meta-analysis results, we explored the effect of combined environmental changes on the cellular elemental content, C:N:P stoichiometry and PIC:C of *E. huxleyi* under two hypothetical scenarios guided by the general characteristics of future oceans projected by climate models (Bindoff et al., 2019; Cooley et al., 2022). Scenario 'Future 1' estimates the effect of combined +CO$_2$ (pCO$_2$ = 720–1000 µatm), warmer sea surface temperatures (+T), higher irradiance (+L) and N deficiency (−N) on *E. huxleyi* stoichiometry. Scenario 'Future 2' assumes the same elevated pCO$_2$, warming and increased light scenario but with P deficiency (−P). These two scenarios are most relevant for low- and mid-latitude open ocean gyres, where nitrogen is typically the primary limiting while phosphate is more likely to be a co-limiting nutrient (Moore et al., 2013). Phosphate concentrations are, however, sufficiently low in oligotrophic regions to cause physiological stress even if growth is not limited (Martiny et al., 2019), for instance in the southwest Pacific, northwest Atlantic and Mediterranean Sea (Duhamel et al., 2021). In high-latitude oceans and most major upwelling regions, iron is the major primary or co-limiting nutrient (Duhamel et al., 2021; Moore et al., 2013) but we have not investigated the effect of iron limitation on *E. huxleyi* stoichiometry in this study.

The effect of multiple, simultaneous environmental changes on *E. huxleyi* stoichiometry could be additive, synergistic or antagonistic. Here, we assumed an additive approach and for each 'future climate' scenario, the L^* value of each cellular parameter (e.g. cellular C or C:N) for the combination of environmental stressors defined above was summed together as follows:

$$L^*_{\text{Future 1}} = L^*_{(+\text{CO}_2)} + L^*_{(+T)} + L^*_{(+L)} + L^*_{(-N)}$$

$$L^*_{\text{Future 2}} = L^*_{(+\text{CO}_2)} + L^*_{(+T)} + L^*_{(+L)} + L^*_{(-P)}$$

For ease of discussion, these future scenario outcomes were also transformed into equivalent percentage change as previously described.

3 | RESULTS

3.1 | The *E. huxleyi* stoichiometry database

The *E. huxleyi* stoichiometry database (EhSD) used for this meta-analysis (Sheward et al., 2023) compiled data on cellular elemental content (PIC, C, N and P) and stoichiometry (PIC:C, C:N, N:P and C:P) extracted from 115 publications that met the inclusion requirements (Tables S1 and S2), which report the results of over 1300 laboratory experiments on 129 globally distributed isolates (Figure S2).

Experimental data in the EhSD are largely derived from North Atlantic isolates (76% of experiments; Figure 1a,b). Of those North Atlantic data, 70% are subpolar isolates from the Norwegian coastline ca. 60° N. Polar, subtropical and tropical strains were less commonly used in publications (Figure 1d,e), accounting for only 0.7%, 12% and 1.0% of the experiments within the EhSD respectively. Overall, the most commonly used strains in the literature were subpolar Norwegian coastline strains PLY B92/11 (373 experiments, 28%) and RCC4522 (83 experiments, 6%), and subtropical Sargasso Sea strain CCMP371 (87 experiments, 6% of full database but accounting for 54% of data derived from subtropical isolates). Of the 129 *E. huxleyi* strains in the EhSD, 30% were only used in one or two experiments.

Carbonate chemistry perturbation experiments were by far the most common type of environmental treatments applied (49% studies; Figure 1c). There is also a strong bias towards cellular PIC and C quantification during experiments (78% and 88% of data in EhSD respectively; Figure 1f) regardless of the environmental treatment applied. Only 14% of the experiments in the EhSD reported cellular P data (Figure 1f) and ca. 10 or fewer publications measured P under temperature, light or pCO$_2$ treatments.

3.2 | Stoichiometry of *E. huxleyi* under control conditions

The mean molar stoichiometry of *E. huxleyi* under control conditions (see Table 1 for definition of control) is 124C:16N:1P when calculated as the ratio between mean cellular organic C of 11.0 ± 6.2 pg cell^{-1}, N of 1.7 ± 1.2 pg cell^{-1} and P of 0.23 ± 0.12 pg cell^{-1} (Figure 2a). When calculated from paired experimental values only (Figure 2b), mean C:N is 7.8 ± 2.6, N:P was 19 ± 8.7 and C:P of 163 ± 66 resulting in a mean C:N:P of 163C:19N:1P. Cellular elemental content shows considerable intraspecific variability. P content is more variable (>fourfold range) than C or N content (Figure 2a) and contributes to the range in N:P and C:P observations (range of 9–32 and 73–268 respectively; Figure 2b). C:N is comparatively better constrained, with 90% of data between 4.4 and 13.0. In some cases, the within-strain C:N:P range under control conditions (from paired experimental data) is almost as high as variability across all strains (e.g. in PLY B92/11, C = 1.6–24.1 pg cell^{-1}, N = 0.3–4.5 pg cell^{-1} compared to C = 1.6–37.9 pg cell^{-1} and N = 0.3–6.4 pg cell^{-1} for *E. huxleyi* as a species). This within-strain variability cannot easily be attributed to the biogeography of different ecotypes, as strains isolated from similar locations (Figure S2) can have dissimilar C:N:P stoichiometry. For example, two high-latitude South Pacific temperate strains NIWA1108 and NZEH have C:N:P of 179:25:1 and 73:11:1 respectively. PIC and C were considered primarily as two distinct carbon pools, as calcite and organic carbon have different roles in the counter carbonate pump and biological carbon pump respectively. Cells generally have less PIC than C (mean PIC:C of 0.89 ± 0.53; Figure 2b) but this is highly variable, with some strains having nearly twice as much PIC as C (95th percentile PIC:C = 1.9).
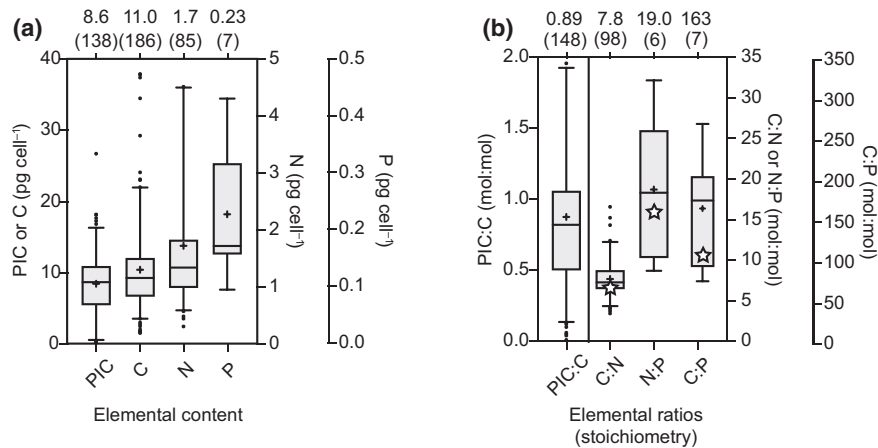
FIGURE 2 Elemental content (a) and PIC:C:N:P stoichiometry (b) of *Emiliania huxleyi* grown under control culture conditions. For the purpose of this meta-analysis, 'control' conditions are defined as no nutrient, temperature, pCO_2 or irradiance stress following Table 1 (see also Supplementary Methods). The number of experiments included are in parentheses. Median values are shown above each plot. Mean values are denoted by '+'. Whiskers represent the 5th–95th percentiles of the data. In (b), white stars denote the 'Redfield ratio' values of C:N = 6.625, N:P = 16, C:P = 106 (Redfield, 1958) for comparison.

3.3 | Response of growth, elemental content and stoichiometry to environmental change

The sensitivity of *E. huxleyi* growth and stoichiometry to environmental change was analysed by calculating the weighted log-transformed response ratio, L^*, for individual environmental drivers that are likely to impact future marine phytoplankton communities: temperature, pCO_2, macronutrient (nitrate and phosphate) limitation and irradiance. Elemental content and C:N:P stoichiometry showed a diverse response to each of these stressors, ranging from no response to >fourfold change (Figures 3 and 4). Briefly, C:N:P stoichiometry responded strongly to macronutrient limitation whereas warming and irradiance had a minimal effect. PIC, C, N and P changed under elevated pCO_2 concentrations but significant responses were predominantly restricted to high and very high pCO_2 levels.

Macronutrient limitation caused the largest shift in C:N:P stoichiometry of all of the environmental stressors considered here but had no significant effect on PIC:C (Figure 3). Under P limitation, a 68% decline in P content combined with an increase in C and N led to a nearly fivefold increase in C:P, a threefold increase in N:P, and a 47% increase in C:N (Table 2). N limitation had a lesser but still large effect on C:N:P stoichiometry, with a 32% decline in N content associated with a doubling of C:N and a (nonsignificant) decline in N:P.

Elevated pCO_2 had no significant overall impact on C:N:P (Table 2) but resulted in generally moderate (ca. 10%) declines in PIC content (i.e. reduced calcification) and increased C content under '+CO_2' conditions of 720–1000 µatm pCO_2 (Figure 3). The negative effect of pCO_2 on cellular calcite rose to −29% under very high ++CO_2 conditions (1000–2000 µatm pCO_2). PIC content and PIC:C both declined by ca. 20%–30% under $pCO_2 > 2000$ µatm (Figure 4). While the majority of individual experiments reported a negative impact of elevated pCO_2 levels on calcification, some studies reported that higher pCO_2 had a positive effect on PIC and PIC:C, particularly where treatment pCO_2

was <1000 µatm (coloured bars, Figure 4). When considered within the context of the results as a whole, the strong response of *E. huxleyi* PIC to elevated pCO_2 concentrations is comparable in magnitude to the decline in PIC under warming (both ca. −30%; Table 2) and is a relatively moderate magnitude of response compared to the effect of nutrient deficiency on cellular P, N:P and C:P (Figure 3).

Low and high light conditions were not associated with significant changes in PIC:C or C:N:P stoichiometry. Light did, however, significantly affect growth rates (−72% under low light, +25% under high light; Figure 3a, Table 2; Table S7). Similarly, increased temperatures increased growth rates by 34% but had little effect on C:N:P stoichiometry overall.

3.4 | Effect of multiple environmental changes on *E. huxleyi* stoichiometry

To explore the potential integrated biogeochemical response of *E. huxleyi* to future ocean change, we estimated whether PIC:C and C:N:P would increase or decrease under future ocean change and by how much by summing individual L^* responses for two future scenarios (see Section 2) that capture several general features of our future oceans as projected by ensemble climate models. Under Future scenario 1 (Figure 5a), our data suggest that climate change could lead to a doubling in C:N (ca. 110%) and declines in N:P and C:P. Future scenario 2 (Figure 5b) indicates that P content will decline by around 60% alongside a 40% increase in C content and moderate decrease in N content. These elemental responses drive a 54% increase in C:N and dramatic increases in N:P (ca. 290%) and C:P (ca. 450%). These two hypothetical future scenarios have opposite effects on C:P and N:P, which decline under N limitation (Future 1) and increase under P limitation (Future 2). Under both future scenarios, elevated pCO_2 and warming will drive a 10–20% decline in PIC and decreasing PIC:C.

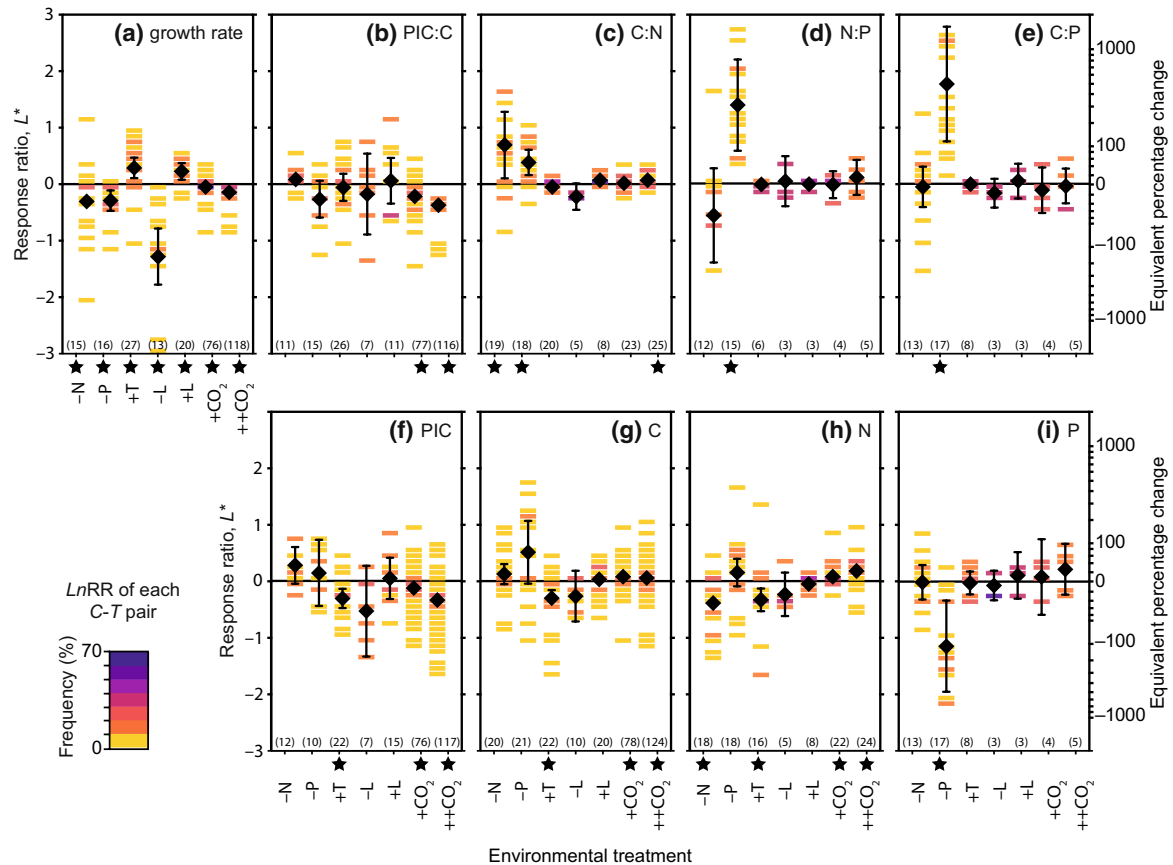**FIGURE 3** Response of *E. huxleyi* growth rate, elemental content and stoichiometry to environmental change. Mean weighted response ratio *L** of (a) growth rate, (b–e) stoichiometric ratios, and (f–i) elemental content, under N deficiency (–N), P deficiency (–P), high temperatures (+T), low irradiance (–L), high irradiance (+L) and two levels of elevated *p*CO₂ concentrations (+CO₂, 720–1000 μatm, and ++CO₂, 1000–2000 μatm). See Table 1 and Supplementary Methods for treatment category definitions. *L** (diamond symbols) is significant if the 95% confidence intervals (bars) do not overlap zero. Stars denote environmental perturbations that produced a significant response from zero. The number of experiments used to calculate *L** are shown in parentheses. The data for +CO₂ (720–1000 μatm) and ++CO₂ (1000–2000 μatm) are also shown in Figure 4. Coloured points represent a percentage frequency histogram of the effect sizes (*Ln*RR; Equation S1, Supplementary Methods) of each individual control (*C*)–treatment (*T*) pair to illustrate the spread of responses in each *L** calculation (see also Figures S3 and S4).

4 | DISCUSSION

4.1 | *Emiliania huxleyi* stoichiometry in context

Emiliania huxleyi exhibits high within-species variability in stoichiometry (Figure 2) and stoichiometric response to environmental change (Figures S3 and S4), which substantiates reports that *E. huxleyi* has strain-specific physiology and biogeochemistry (e.g. Blanco-Ameijeiras et al., 2016; Langer et al., 2009). This strain specificity is frequently attributed to the unusually large genome of *E. huxleyi*, which may enable greater phenotypic variability (Read et al., 2013). For instance, recent experiments by Villiot et al. (2021) reported that mean C:N ranged between ca. 4 and 18 across seven coccolithophore species, which is comparable to the range in C:N observed here under control conditions (3–17; Figure 2b) across the *E. huxleyi* strains synthesised in the EhSD. PIC:C also shows substantial intraspecific variability (<0.1–3.3; Figure 2b) in agreement with previous data collations (*E. huxleyi*

PIC:C of 0.1–2.7; Krumhardt et al., 2017) and variable degrees of coccolith calcification observed across *E. huxleyi* morphotypes (Young et al., 2003). This PIC:C range may be a relatively conservative feature of coccolithophore biogeochemistry as it also broadly reflects the PIC:C range reported for many fossil calcareous nannoplankton species (Gibbs et al., 2018). The mean *E. huxleyi* PIC:C of 0.88 ± 0.54 is therefore likely to be a reasonable proxy for the PIC:C of other extant coccolithophore species, particularly species with similar morphological characteristics and degrees of calcification (e.g. *Gephyrocapsa*). Data from laboratory experiments suggest that the PIC:C of *E. huxleyi* may be less representative of 'heavily calcified' taxa, such as *Calcidiscus* spp. and *Helicosphaera* spp. (Diner et al., 2015; Gafar et al., 2019; Šupraha et al., 2015). PIC:C and C:N:P data for the majority of other extant coccolithophore species are currently lacking, largely because many species are not maintained in culture. Given the intraspecific variability seen here for *E. huxleyi* (Figure 2; Figures S3 and S4), the limited amount of available data from other coccolithophore species that
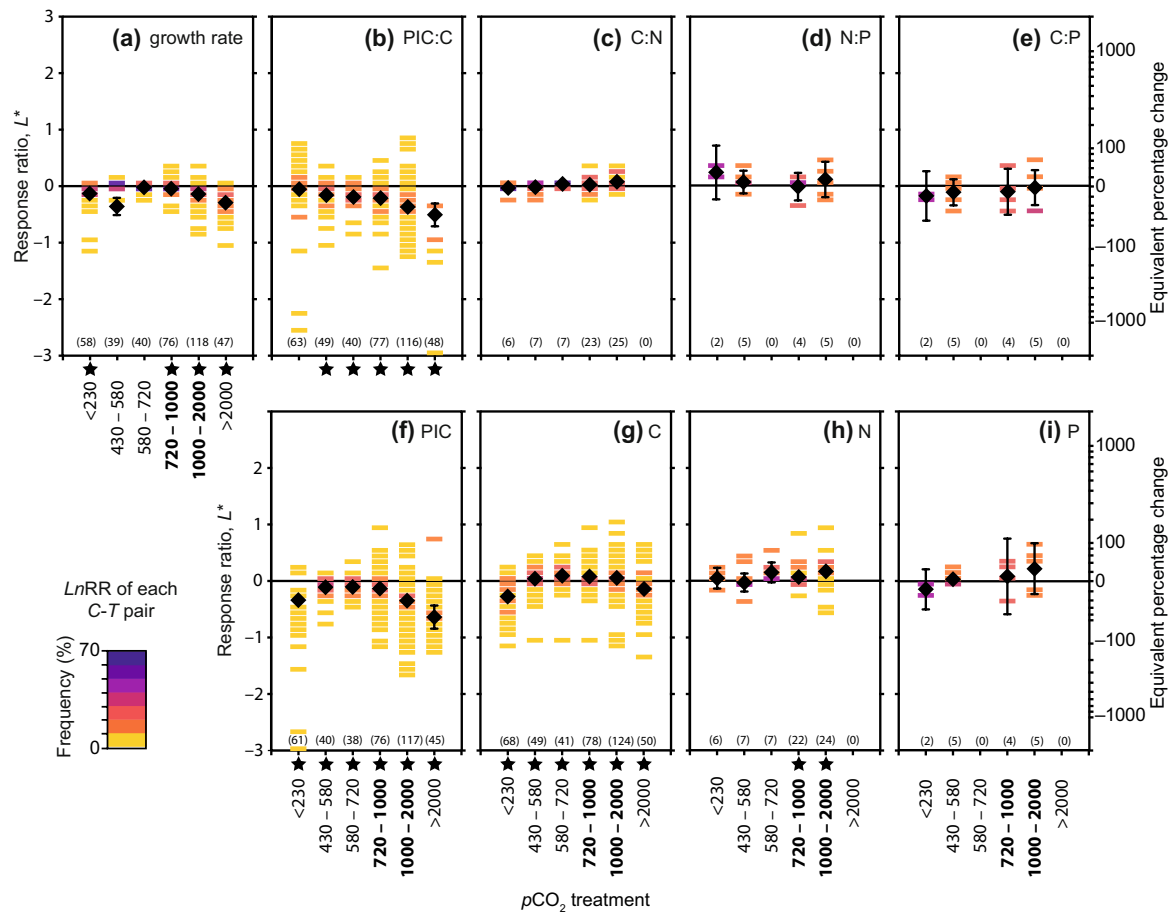
FIGURE 4 Response of *E. huxleyi* growth rate, elemental content, and stoichiometry to a range of future pCO_2 conditions (μatm). Mean weighted response ratio L^* of (a) growth rate, (b–e) stoichiometric ratios and (f–i) elemental content, under six pCO_2 concentration levels (see Table 1 and Supplementary Methods for treatment category definitions). L^* (diamond symbols) is significant if the 95% confidence intervals (bars) do not overlap zero. Stars denote elevated pCO_2 levels that produced a significant response from zero. The number of experiments used to calculate the means are shown in parentheses. The data for pCO_2 treatment levels 720–1000 and 1000–2000 μatm are replicates of the L^* result for +CO₂ and ++CO₂, respectively, shown in Figure 3. Coloured points represent a percentage frequency histogram of the effect sizes (*Ln*RR; Equation S1, Supplementary Methods) of each individual control (*C*)–treatment (*T*) pair to illustrate the spread of responses in each L^* calculation (see also Figure S4).

nevertheless indicates a degree of interspecific variability in PIC:C (e.g. Krumhardt et al., 2017) and C:N:P (Villiot et al., 2021) across at least some extant species, and the fact that *E. huxleyi* is an atypical coccolithophore in some respects (notably bloom forming), the continued use of *E. huxleyi* as a representative species for coccolithophores may need to be revisited in future in order to best characterise the contribution of coccolithophore calcification and production to biogeochemical cycles.

The mean *E. huxleyi* C:N:P of 124C: 16N: 1P (C:P = 124; C:N = 7.6, N:P = 16) is close to Redfield values (Redfield, 1958) for mean elemental composition of marine particulate organic matter (C:P = 106, C:N = 6.6, N:P = 16) but implies that *E. huxleyi* is enriched in C per unit P relative to Redfield and towards the upper range of reported values for nutrient-replete marine phytoplankton cultures (C:P 27–135 and N:P 5–9; Geider & La Roche, 2002). The relatively low P requirements of *E. huxleyi* shown here (Figure 2a) and its low half-saturation constants for nitrate and phosphate (0.14–0.35 μM and 0.051–0.31 μM respectively; Krumhardt et al., 2017) likely contribute to

the ability of *E. huxleyi* to thrive under a range of nutrient regimes, including oligotrophic conditions.

Based on available data for other important plankton groups, *E. huxleyi* C:P and N:P is generally higher than the mean values for both dinoflagellates (C:P = 90, N:P = 12) (Carnicer et al., 2022; Finkel et al., 2016) and diatoms (C:P = 101, N:P = 15) but lower than that of cyanobacteria (C:P = 121–165, N:P 21–33) (Bertilsson et al., 2003; Sharoni & Halevy, 2020). Comparisons between the stoichiometry of *E. huxleyi* and non-calcifying phytoplankton must also account for the fact that, for the same amount of nutrients fixed into only organic C by non-calcifying phytoplankton, coccolithophores biosynthesise both organic and inorganic C with little additional N requirement compared to non-calcifying phytoplankton (mean *E. huxleyi* C:N = 7.6 compared to, e.g. mean C:N = 6.4 reported by Garcia et al., 2018 for 12 diatom strains). From this alternate perspective, combining PIC and C pools (total cell C, TC) gives a mean TC:N:P of 221TC:16N:1P, TC:N of 13.6 and TC:P of 221, which is approximately double the C:N and C:P of Redfield (6.6 and 106 respectively). This is attainable

TABLE 2 Mean percentage change (converted from L^*) of *E. huxleyi* growth rate (μ), PIC:C and C:N:P stoichiometry, and elemental content (PIC, C, N and P) in response to environmental change.

	μ	PIC:C	C:N	N:P	C:P	PIC	C	N	P
−N	−26	+32	+101	-43	−5	+32	+14	−32	−1
−P	−25	−23	+47	+305	+493	+15	+67	+17	−68
+T	+34	−5	−5	−1	−0.3	−27	−26	−28	−2
−L	−72	−16	−20	+4	−15	−41	−23	−21	−6
+L	+25	−17	−8	−1	+5	5	+3	−5	+12
<280	−12	−6	−4	+26	−17	−28	−24	+6	−13
430–580	−30	−15	−2	+6	−11	−15	+4	−2	+3
580–720	−2	−18	+3	—	—	−9	+10	+17	—
+CO$_2$	−4	−19	+2	−2	−11	−12	+8	+8	+9
++CO$_2$	−13	−31	+7	+11	−4	−29	+6	+20	+25
>2000	−26	−40	—	—	—	−47	−13	—	—
Future scenario 1[a]	+18	−11	+110	−46	−11	−11	−6	−49	+18
Future scenario 2[b]	+20	−37	+54	+287	+456	−22	+39	−3	−62

Note: Significant changes (where the 95% confidence interval of L^* does not cross zero) are highlighted in colour (blue negative change, red positive change).

'—' denotes that no experiments met the criteria for the L^* calculation of this environmental category. Definitions of the environmental categories listed are shown in Table 1.

[a]Future scenario 1 is the overall additive mean response to combined elevated pCO$_2$ (+CO$_2$, 720–1000 µatm), warming (+T), high irradiance (+L) and N deficiency (−N).

[b]Future scenario 2 is the overall additive mean response of each ratio or elemental content to combined +CO$_2$, +T, +L and P deficiency (−P). Both future scenarios are presented in Figure 5.

partly because calcification has relatively low net nutrient costs (coccolith polysaccharides have low N requirements and coccolith production continues even if cell division ceases under nutrient starvation; Monteiro et al., 2016 and references therein). However, as some calcification-supporting structural and functional biomolecules (e.g. the protein-rich CaCO$_3$ crystal growth matrix; Mackinder et al., 2011) do have a significant N requirement, coccolithophores are also likely to support calcification through the efficient use and retention of their cellular N content (e.g. Villiot et al., 2021).

These mean C:N:P differences across major plankton groups and Redfield values more generally may reflect interactions between phytoplankton stoichiometry and biogeography and the potential role of stoichiometry in influencing the taxonomic and size structure of phytoplankton communities. Coccolithophores thrive in oligotrophic conditions (Balch, 2004; Follows et al., 2007; Krumhardt et al., 2017) and the C:N:P of *E. huxleyi* shown here aligns with its intermediate size and biogeography relative to other major plankton groups. Marine cyanobacteria (mostly picophytoplankton) with relatively higher C:P and N:P typically dominate oligotrophic subtropical gyres and, in contrast, diatoms and dinoflagellates with generally larger cells typically dominate in nutrient-rich, upwelling regions (Marañón, 2015). A refined definition of the mean and variable C:N:P of coccolithophores and other major plankton groups has the potential to inform predictive models of ocean biogeochemistry that parameterise phytoplankton functional groups and incorporate known global variations in phytoplankton growth conditions and biogeography (Follows & Dutkiewicz, 2011).

4.2 | Macromolecular framework for C:N:P responses to environmental change

Cellular elemental content is underpinned by the composition of proteins, carbohydrates, lipids, nucleic acids and pigments that contain different quantities of C, N and P. Adjustments to this macromolecular composition form part of cellular responses to dynamic environmental conditions and drive changes to C:N:P stoichiometry (Geider & La Roche, 2002). Existing macromolecular data for *E. huxleyi* can therefore provide a mechanistic framework to explain the biochemical mechanisms underlying C:N:P responses observed in our analysis. The substantial plasticity in *E. huxleyi* C:N:P with macronutrient limitation (Figure 3) is consistent with shifts in macromolecular allocation reported from P-starved and N-starved cultures. Under P limitation, cell division ceases (Müller et al., 2008) and the synthesis of P-rich nucleic acids and membrane phospholipids decreases (Wördenweber et al., 2017), dramatically decreasing cell P content while C and N show little change or a slight increase in C is observed related to storage accumulation (Geider & La Roche, 2002; Tanioka & Matsumoto, 2020). Similarly, we observed that N limitation led to a decline in N content, decreased N:P and increased C:N and C:P that is consistent with reported declines in N-rich protein synthesis (Mckew et al., 2015; Rokitta et al., 2014) in N-limited *E. huxleyi* cultures and increased accumulation of storage C that is generally observed among N-limited microalgae (Geider & La Roche, 2002).

There is good empirical and mechanistic support for temperature as a driver of significant stoichiometric change through its
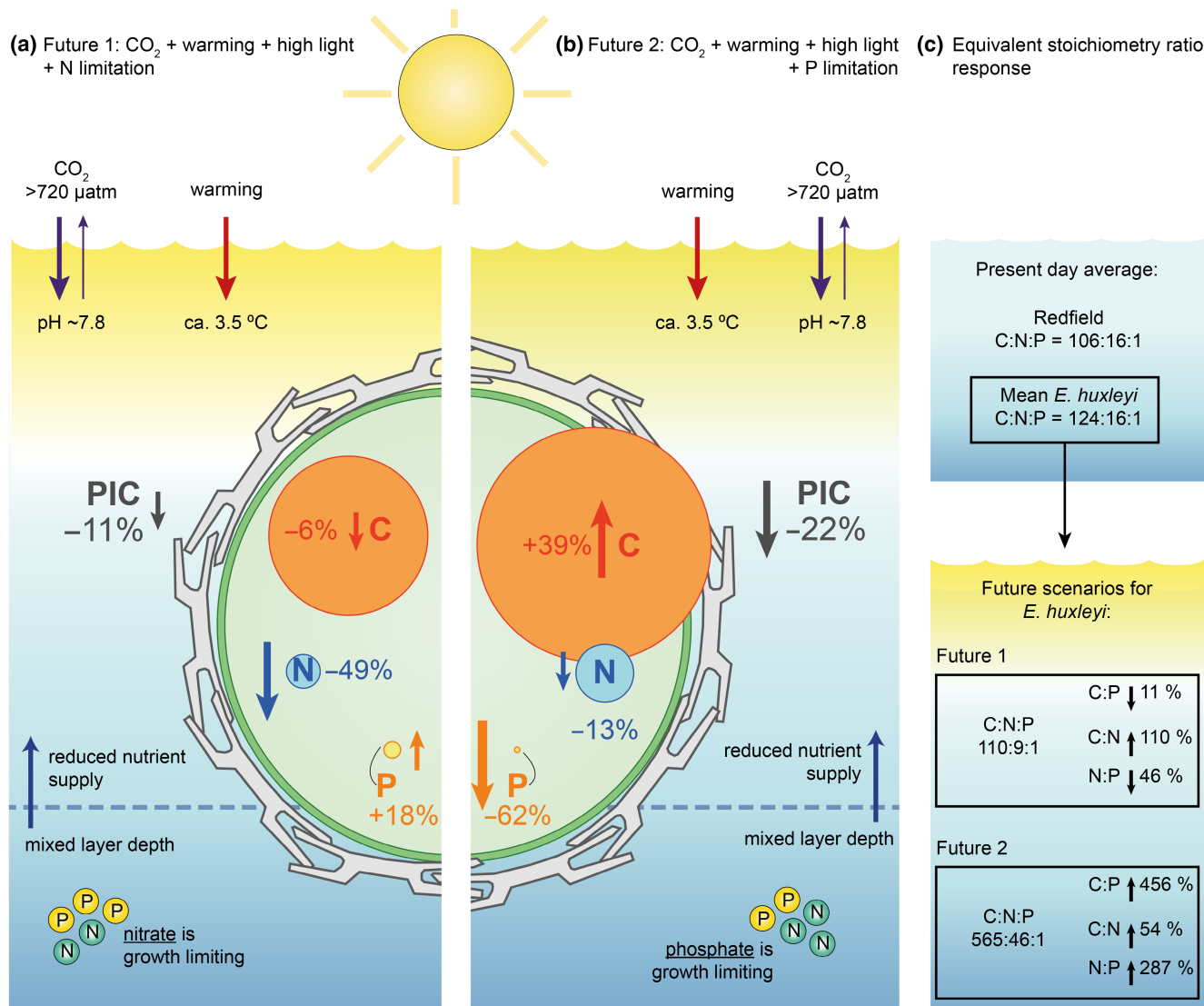
FIGURE 5 The response of *E. huxleyi* stoichiometry to global ocean change, circa the year 2100. The impact of future global ocean change on cellular PIC, C, N and P content in *E. huxleyi* is synthesised (additive) from the magnitude of responses (L^*) to individual environmental stressors in laboratory cultures. In (a), scenario 'Future 1' of warming, elevated $p\mathrm{CO_2}$ (720–1000 µatm) and higher irradiance in a region of N deficiency is shown. In (b), the same scenario is shown but for a region of P deficiency ('Future 2'). Ocean conditions in the year 2100 are projected to be characterised by acidification and ocean warming, which intensifies stratification, enhances nutrient limitation in the photic zone and increases light exposure to phytoplankton distributed at shallower depths (e.g. Cooley et al., 2022, see Section 2). For context, we indicate the magnitude of warming and pH change broadly indicated by climate models for 2100 under high emission scenarios (RCP8.5/SSP5-8.5; e.g. Kwiatkowski et al., 2020) The depicted 'size' of cellular C content (orange pools), N content (blue pools), and P content (yellow pools) corresponds to the relative amount of C, N and P in *E. huxleyi* under control conditions that is subsequently scaled to the magnitude (%) change in C, N and P content calculated for Future 1 and Future 2 scenarios. (c) The equivalent present-day mean C:N:P according to Redfield (1958) and for *E. huxleyi* under non-limiting conditions (Figure 2) are shown in the upper panel and the resulting C:N:P of *E. huxleyi* under Future 1 and Future 2 scenarios are shown calculated from the change in L^*.

effect on P-rich ribosome content (Yvon-Durocher et al., 2015). However, such an effect was not apparent for *E. huxleyi* in our analysis. Warmer temperatures increase protein synthesis efficiency and may allow fewer ribosomes to maintain equivalent growth rates, which has been invoked as a mechanism for decreased P content as well as higher C:P and N:P with increased temperature that has been observed across ocean regions (Moreno & Martiny, 2018; Toseland et al., 2013; Yvon-Durocher et al., 2015). Recent work by Zhang et al. (2021) supports this hypothesis for one strain of *E.*

huxleyi, where increased temperature (and growth rate) caused increased C:P and N:P that in turn corresponded to increased C:RNA and Protein:RNA respectively. This study (Zhang et al., 2021) additionally showed little apparent effect of temperature on C content and PIC:C in *E. huxleyi*. In contrast, our meta-analysis found no clear effect of temperature on P content or C:N:P, but did show decreased C and PIC content with increased temperatures. This latter result could reflect the negative relationship between temperature and C storage observed in other microalgae (Geider et al., 1998; Raven &

Geider, 1988). Temperature has been shown to have mixed effects on C:N:P over a broad range of phytoplankton taxa, cause considerably smaller stoichiometric change than macronutrient limitation (Tanioka & Matsumoto, 2020; Yvon-Durocher et al., 2015) and equated no effect of temperature on coccolithophore C:N:P when considered in aggregate (Tanioka & Matsumoto, 2020). Considering this uncertainty in phytoplankton C:N:P response to temperature and the relatively high stoichiometric plasticity of *E. huxleyi*, our findings of no apparent impact of temperature on C:N:P are unsurprising and do not refute the effect of temperature on C:N:P in other taxa or across ocean regions that have been suggested by others (Toseland et al., 2013; Yvon-Durocher et al., 2015).

4.3 | *Emiliania huxleyi* biogeochemistry under future climate change

Earth system models project that climate change over the next 60–80 years will be associated with an approximate doubling of present-day CO_2, consequently reducing ocean pH and carbonate saturation states and increasing sea surface temperatures by several degrees Celsius (Fox-Kemper et al., 2021; Kwiatkowski et al., 2020). Warmer oceans will likely lead to reduced vertical mixing and enhanced density-driven stratification that will change surface ocean nutrient concentrations (Bindoff et al., 2019; Fox-Kemper et al., 2021) and influence the depth habitat and, subsequently, the light conditions experienced by phytoplankton communities. Coccolithophores diversified in the warm, oligotrophic oceans of the Mesozoic and early Cenozoic (Lowery et al., 2020) and are generally considered be good competitors under oligotrophic conditions (Balch, 2004). *Emiliania huxleyi* evolved relatively recently and is a bloom-forming species with a global distribution that indicates a broad tolerance of environmental conditions.

To explore how concurrent future changes in ocean conditions may impact *E. huxleyi* PIC:C and C:N:P, we defined two future ocean scenarios with combined environmental changes (increased temperature, increased light, elevated pCO_2 and either N deficiency or P deficiency) and summed the relevant L^* results from our meta-analyses of each environmental category (Figure 5; Table 2). The strong shift in *E. huxleyi* stoichiometry under nutrient limitation (Figure 3) already shown by our meta-analysis indicates that the spatial extent and severity of N availability (Future 1) and P availability (Future 2) will likely be a major driver of the future biogeochemical role of *E. huxleyi*. Earth system models project a 9–14% decrease in nitrate concentrations in the surface 100 m of the ocean by 2080–2100 under RCP8.5 emission scenarios (Bindoff et al., 2019). Phosphate is typically a co-limiting nutrient but phosphate concentrations are low in oligotrophic regions (Moore et al., 2013) and are also expected to decrease with climate change (Boyd, Lennartz, et al., 2015). As phytoplankton productivity is primarily limited by N (and P secondarily) in mid- and low-latitude oceans (Moore et al., 2013), an increased *E. huxleyi* cellular C:N (both scenarios) and C:P (Future Scenario 2) indicates that in these often oligotrophic subtropical regions, climate

change has the potential to enhance the C content of exported *E. huxleyi*-derived organic matter relative to the available nutrients via more nutrient-efficient *E. huxleyi* C production (increased growth rate of ca. 20%, Table 2). Increased C:N combined with increased growth rates under 'climate change'-type scenarios have also been reported for other phytoplankton groups (Velthuis et al., 2022). In oligotrophic subtropical regions, warming- and irradiance-driven enhancement of C fixation for available N by phytoplankton (Galbraith & Martiny, 2015) may act to offset some of the biogeochemical and ecological consequences of the broad decline in net primary production (ca. −4% to −11% relative to 2006–2015) and export production (ca. −9% to −16% relative to 2000) (Bopp et al., 2013; Kwiatkowski et al., 2018) projected by 2100 under RCP8.5 emission scenarios by climate models (Bindoff et al., 2019). Increasing C:P and C:N under climate change will likely also have ecological consequences through reduced food quality for zooplankton and invertebrates, where their energy requirements are met but their nutrient requirements are not met (Boersma et al., 2008). This can reduce the efficiency of zooplankton grazing and energy transfer to higher trophic levels (Kwiatkowski et al., 2018).

Ocean acidification has generally been thought to be detrimental to coccolithophore calcification, causing concern that coccolithophores are highly sensitive to ocean acidification (Kroeker et al., 2013; Meyer & Riebesell, 2015; Seifert et al., 2020). Our results confirm that elevated pCO_2 levels have a negative impact on cellular calcification and PIC:C (Figure 4; Findlay et al., 2011; Krumhardt et al., 2017; Meyer & Riebesell, 2015; Ridgwell et al., 2009). Both seawater CO_2 concentrations and alkalinity are sensitive to changes in coccolithophore calcification, a process that produces CO_2 (by converting two bicarbonate ions into one $CaCO_3$ and one CO_2 molecule) and removes alkalinity from the surface ocean, thus reducing its capacity to buffer changes in CO_2. The PIC:C of exported organic matter (the so-called 'rain ratio') is a major determinant of CO_2 flux between the surface ocean and the atmosphere (e.g. Ridgwell et al., 2009; Rost & Riebesell, 2004). The decrease in *E. huxleyi* PIC and PIC:C suggested for the future by our synthesis (Figure 5; Table 2) may therefore influence surface ocean chemistry and marine carbon cycle dynamics, especially in regions where *E. huxleyi* is a substantial component of phytoplankton communities.

Translating this synthesis of laboratory results to natural systems requires careful consideration: predicting future *E. huxleyi* biogeochemistry solely from observations of single strains during short-term exposure (weeks to months) to individual environmental stressors is an obvious simplification of both the complex marine environment and genetically diverse natural populations. One caveat to our synthesis approach is that synergistic or antagonistic effects may arise under 'multi-stressor' conditions (Boyd et al., 2018; Seifert et al., 2020), not just the additive effect of multiple environmental drivers that we have assumed for our analysis. Synergistic or antagonistic responses to multiple stressors are indicated by some studies that have undertaken bi- or multi-stressor experiments (listed in Table S2). For instance, our meta-analysis indicates that overall, warming and higher light as individual stressors had no

significant effect on C:N:P (Figure 3). However, when higher light treatments were combined with elevated pCO$_2$, *E. huxleyi* growth rates were observed by Seifert et al. (2020) to increase to a lesser extent than under increased light alone (antagonistic effect) and by Feng et al. (2020) to decrease to a greater extent than under increased light alone (Feng et al., 2018, negative synergistic effect). The multi-stressor study by Feng et al. (2020) additionally indicated that synergistic effects on growth rate, cellular PIC and cellular N were more common under combined N limitation and elevated pCO$_2$ than under N limitation alone. Nutrient limitation has also been reported to amplify the CO$_2$-driven increase in C:N and C:P in a recent phytoplankton meta-analysis (Velthuis et al., 2022). Given the range of responses of *E. huxleyi* elemental content and stoichiometry to individual stressors across the strains in the EhSD (Figures S3 and S4) and strain-specific responses reported in the literature (e.g. Langer et al., 2009) and the genetic diversity of *E. huxleyi* (Read et al., 2013), future research should ideally prioritise experimental designs that systematically test strain-specific additive, synergistic or antagonistic responses.

A second caveat to this synthesis approach is that not all climate-relevant environmental factors were investigated in our future scenarios, as the environmental categories used for the meta-analysis were somewhat constrained by the range of treatment conditions preferentially applied in the literature (Figure 1). For example, iron scarcity is an important driver of phytoplankton productivity, particularly in the Southern Ocean, and climate change is expected to alter both the sources of iron to the ocean and its bioavailability to phytoplankton through the impacts of changing ocean chemistry on the chemical speciation of iron in seawater (Hutchins & Boyd, 2016). However, the effect of iron or other trace metal availability on *E. huxleyi* stoichiometry has not been investigated here due to the limited amount of data available in the EhSD.

On longer timescales relevant for capturing adaptation, *E. huxleyi* has also demonstrated an initial potential for growth rates, calcite and biomass production to adapt to ocean warming and acidification through phenotypic plasticity (Schlüter et al., 2014) although this may partly revert on multi-year timescales (Schlüter et al., 2016). Biotic–trophic interactions must also be considered, as spatial variability in changing conditions combined with species-specific stoichiometric and growth responses to environmental stressors will affect resource competition and top-down pressures. These interactions are likely to alter the biogeography and productivity of key phytoplankton groups (Boyd, Lennartz, et al., 2015; Henson et al., 2021), influencing the relative contribution of *E. huxleyi* and other coccolithophores to primary production in different regions. For example, interactive effects of warming, elevated CO$_2$ and P deficiency combined with silicate limitation under climate change has been suggested to favour coccolithophores over diatoms in the northern North Atlantic (Boyd, Lennartz, et al., 2015).

The meta-analysis of laboratory stoichiometry data is a valuable source of information for understanding the physiological responses, including stoichiometry, of marine phytoplankton to environmental change. This provides crucial insights into patterns and trends in marine ecosystem functions and the spatial and temporal characteristics of phytoplankton communities both now and under different climate conditions. Looking forwards, prioritising well-designed multi-stressor experiments (Boyd et al., 2018; Seifert et al., 2020) that simulate relevant levels of a wider range of environmental drivers and reduce biogeographic strain bias (Figure 1; Figures S2–S4) will address some of the caveats raised in our meta-analysis and improve confidence in projections of *E. huxleyi* stoichiometry responses to climate change. Equally, research into the variable C:N:P and PIC:C stoichiometry of a broader diversity of coccolithophore species will better inform our understanding of the consequences of climate change for coccolithophore contributions to marine biogeochemical cycles.

5 | CONCLUSIONS

Emiliania huxleyi demonstrates a broad spread of C:N:P stoichiometry under control conditions and our meta-analysis reveals variable effects of individual climate-relevant environmental drivers on cellular elemental content, PIC:C and C:N:P stoichiometry, ranging from no overall effect to greater than a fourfold change (e.g. cellular P content under P deficiency). *E. huxleyi* therefore likely has substantial scope for stoichiometric plasticity under environmental change and this flexibility likely contributes to its ability to thrive under a broad spectrum of environmental conditions. In a future scenario where pCO$_2$, temperature, and light intensity in the ocean increase and nutrient availability decreases, the combined results of our meta-analysis suggest that *E. huxleyi* will decrease PIC:C, increase C:N, and N:P and C:P will either increase under P limitation or decrease due to N limitation. Decreasing PIC:C (i.e. promoting photosynthesis over calcification) would reduce the ratio of CaCO$_3$ to C exported in sinking biogenic material and therefore whether *E. huxleyi* acts as a net exporter of carbon to the deep ocean. While there are caveats to our synthesis, our results provide a comprehensive indication of the potential consequences of global ocean change for the stoichiometry of a ubiquitous coccolithophore species, thus informing our understanding of its future role in marine biogeochemical cycles. Implementing an improved range of variable stoichiometry for key phytoplankton groups within biogeochemical and Earth system models may better replicate global patterns in marine phytoplankton C, N and P while illuminating the biochemical mechanisms underlying phytoplankton functional trait trade-offs in present and future ecosystems.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Zenodo at https://doi.org/10.5281/zenodo.7594880.

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