



Subtropical gyres dominate global calcium carbonate production by coccolithophores

Nicola A. Wiseman^{1,2}, Joost de Vries², Alex J. Poulton³, Nichole L. J. Marsh³, Levi J. Wolf¹, and Fanny M. Monteiro^{1,4}

¹School of Geographical Sciences, University of Bristol, Bristol BS8 1SS, UK.

²Department of Earth, Ocean, and Ecological Sciences, University of Liverpool, Liverpool L69 3GP, UK.

³The Lyell Centre for Earth and Marine Science, Heriot-Watt University, Edinburgh EH14 4AS, UK.

⁴Centre for ice, Cryosphere, Carbon and Climate (iC3), Department of Geosciences, UiT The Arctic University of Norway, 9019, Tromsø, Norway.

Correspondence: Nicola A. Wiseman (nicola.wiseman@liverpool.ac.uk)

Abstract. Marine calcifying phytoplankton known as coccolithophores are a key part of the ocean carbon cycling, contributing to both the export of organic matter via the biological pump and the establishment of the vertical seawater alkalinity gradient known as a the carbonate counter pump. As dominate producers of calcium carbonate production, the rate at which coccolithophores produce calcium carbonate, determines the magnitude of the carbonate counter pump, and is sensitive to future changes in temperature, pH, and nutrient and light availability. Our understanding of spatiotemporal distributions of calcium carbonate production is limited, as measuring calcium carbonate production at sea is labour-intensive, and currently biased both seasonally and spatially. Here we leverage novel machine learning techniques to predict calcium carbonate production on a global scale to a depth of 200m, providing resolution with depth that has not been possible for previous remote sensing based approaches. We find a global integrated annual production of $1.23 \text{ Pg C yr}^{-1}$ [0.78-1.71], with the majority (59%) occurring in the subtropical gyres, challenging the dominance of more-often studied high latitude bloom regions. Our model also shows 18% of global annual CP occurring below the euphotic zone. Our results highlight the need for additional sampling and process studies in the subtropical gyres and at low lights levels/deep in the water column in particular to further constrain our understanding of the ocean carbonate cycle.

1 Introduction

Calcium carbonate (CaCO_3) is an integral component of the global carbon cycle. In the surface ocean, CaCO_3 production produces CO_2 , resulting in a decreased ocean CO_2 uptake capacity on short timescales (Robertson et al., 1994). In marine sediments, CaCO_3 can buffer changes in atmospheric carbon dioxide (CO_2) via dissolution on thousand-year timescales (Archer et al., 1998; Broecker and Takahashi, 1977). Thus, changes in the production, export and burial of CaCO_3 impact atmospheric CO_2 on both long and short timescales.

Coccolithophores are photosynthetic plankton that form calcium carbonate platelets called coccoliths. Surface calcium carbonate production by coccolithophores generates a calcium carbonate driven vertical gradient in seawater alkalinity which



influences air-sea CO₂ uptake, known as the carbonate counter pump (Neukermans et al., 2023). Particulate calcium carbonate may impact the biological carbon pump via ballasting (Ziveri et al., 2007). The process of calcification may also be sensitive to changing light, temperature, nutrients, and ocean acidification, providing a feedback on ocean carbon uptake in a changing climate (Beaufort et al., 2011; Krumhardt et al., 2019; Gafar et al., 2019; Kottmeier et al., 2022).

Previous estimates of global coccolithophore calcium carbonate production (CP) have come from two primary methods: basin-scale extrapolation or remote sensing algorithms. Satellites provide much needed spatiotemporal estimates of CP, but involve many levels of assumptions in order to derive CP from remote sensing reflectance. Satellite CP algorithms rely on multiple satellite-derived products, including PIC, chlorophyll-*a*, and sea-surface temperature (SST), which each have their own required assumptions and associated errors. The two-band PIC algorithm is the most uncertain of these products, as it relies on absolute water-leaving radiances, rather than ratios between radiances like other products, and is therefore more susceptible to error in atmospheric correction (Balch et al., 2005). Additionally, the remote sensing reflectance properties used for estimating PIC are based primary on the optical properties of the cosmopolitan coccolithophore *Gephyrocapsa huxleyi*. However, the work by de Vries et al. (2025b), which modeled the carbon stocks of top 58 most abundant coccolithophore species found that *G. huxleyi* only accounted for 7% of global integrated coccolithophore inorganic carbon stocks with large and heavily calcifying coccolithophores dominating the stock. Additionally, PIC from satellites includes detached coccoliths (Balch and Mitchell, 2023; Neukermans et al., 2023) which can make substantial contributions to PIC concentrations in the ocean (de Vries et al., 2025b). These assumptions could result in biases in both the distribution and magnitude of CP estimated from space.

The first satellite algorithm from Balch et al. (2007) estimated CP using an empirical relationship derived from *in situ* ¹⁴C CP rate observations. Specifically, they derived a least-squares multiple linear regression relating CP to sample depth, particulate inorganic carbon (PIC) concentration, chlorophyll-*a*, day length, and temperature. Balch et al. (2007) then used MODIS-Terra monthly products for PIC, chlorophyll-*a*, and SST to predict CP globally, which they then integrated to the depth of the euphotic zone (Zeu) (also derived from the satellite chlorophyll-*a* product following Morel (1988)) assuming a constant calcium carbonate production rate throughout the euphotic zone. Balch et al. (2007) derived uncertainty estimates from the error of satellite-derived chlorophyll from O'Reilly et al. (1998) which propagates through the Morel (1988) Zeu calculation. They then also assume an error on the calcification estimates of 10% based on potential atmospheric-related errors, resulting in a total error of approximately $\pm 20.5\%$ for a total global calcium carbonate production of $1.6 \pm 0.3 \text{ Pg C yr}^{-1}$. Hopkins and Balch (2018) estimated surface CP rates from satellite-derived particulate inorganic carbon coupled with a phytoplankton growth model. This approach is based on the carbon-based productivity model of Behrenfeld et al. (2005), which derives net primary production from carbon concentration, growth rate, euphotic zone depth, and an irradiance function. Hopkins and Balch (2018) modified this model to predict CP rates as a function of particulate inorganic carbon (PIC) concentration, a coccolithophore-specific growth rate function, irradiance, and depth. They assumed that the growth rate function is dependent on temperature and light without nutrient limitation, and that CP decreases with light availability through the water column. Additionally, they assumed that coccolithophores, primarily *G. huxleyi*, dominate the satellite PIC signals. When integrating to the depth of the euphotic zone, they assume a Beer's law-type relationship such that CP will decay with light, using the diffuse



attenuation coefficient at 490 nm (K_d490) from satellite measurements. They then applied this function to Aqua MODIS products for SST, PIC, PAR, and K_d490 , giving a global calcium carbonate production estimate of $1.42 \pm 1.69 \text{ Pg C yr}^{-1}$. It is not mentioned how their error was estimated.

60 Some field campaigns that have measure CP have attempted to estimate globally integrated production by calculating the ratio of CP by coccolithophores to net primary production (PP) in each sample (both measured using ^{14}C techniques). They then calculate a mean CP/PP ratio, which is then multiplied by an estimate of global PP to approximate global CP. Estimates attributed to Poulton et al. (2006) by Berelson et al. (2007) used this method, which resulted in ratio of $0.06 \text{ mol mol}^{-1}$ CP/PP multiplied by an estimated primary production of 50 Pg C yr^{-1} , giving a global annual calcium carbonate production
 65 of 3.0 Pg C yr^{-1} . In Marañón et al. (2016), data is compiled from the global Malaspina expedition, which consisted of seven transects circumnavigating the tropical and subtropical ocean. Calcium carbonate production and primary production rates were measured using the ^{14}C -uptake and microdiffusion technique (MDT). They calculated a CP/PP ratio of $0.05 \pm 0.04 \text{ mol mol}^{-1}$ and a global primary production estimate of $48.5 \text{ Pg C yr}^{-1}$ from Field et al. (1998) to extrapolate a global calcium carbonate production of 2.4 Pg C yr^{-1} . Daniels et al. (2018) follows the same assumptions as Marañón et al. (2016), but with
 70 a global compilation of calcium carbonate production rates. They calculate a geometric mean CP/PP ratio of $0.02 \text{ mol mol}^{-1}$ and use a global primary production of 50 Pg C yr^{-1} for a global CP estimate of 1.0 Pg C yr^{-1} .

One slightly different approach from Ziveri et al. (2023) measured the calcium carbonate content of living pelagic calcifiers, including coccolithophores, foraminifera, pteropods, and heteropods in the North Pacific. They then used the estimated turnover time for each group from a compilation of laboratory experiments to calculate an approximate calcium carbonate pro-
 75 duction rate which they extrapolate globally under the assumption that the low calcium carbonate stock region they sampled is representative of 87% of the global ocean, which gave a global calcium carbonate production of 2.6 Pg C yr^{-1} for the calcifier community sampled, 67–97% of which they expected to be from coccolithophores due to their shorter turnover time compared to other calcifying groups.

In situ measurements are too sparse for traditional linear data interpolation methods, with strong seasonal and regional
 80 biases (Daniels et al., 2018). Extrapolation from basin scale estimates does not cover the spatial or temporal variability in CP. This method is subject to bias from sampling location and time, as CP is typically only measured during cruises where CP is expected to be occurring, as it is a very intensive measurement to make due to the requirement to add 5-10 times more ^{14}C than is needed to measure primary production to overcome the 20 to 50-fold difference in their absolute rates (Daniels et al., 2018). Extrapolating from these measurements is likely to then overestimate global CP as it would miss the
 85 biogeography and seasonality of coccolithophore growth. Additionally, these measurements only give a singular integrated total estimate, and lack the spatial context needed to constrain processes based models. The spatial patterns of calcite production are important to capture as calcite production impacts air-sea CO_2 flux by altering the carbonate system equilibrium (Shutler et al., 2013; Iglesias-Rodríguez et al., 2002). For example, during calcification, 40% more CO_2 is released in polar vs tropical surface waters as the amount of CO_2 released per mol of calcium carbonate produced increases in colder waters (Smith, 2013;
 90 Smith and Gattuso, 2011). Where these calcium carbonate is produced within the water column also determines how long the carbon remains out of contact from the atmosphere (Tamsitt et al., 2017; DeVries and Primeau, 2011). The spatial patterns of



calcium carbonate production have first order impacts on the carbonate counter pump. Therefore, it is important to resolve the spatiotemporal patterns of CP to properly capture the feedback with air-sea CO₂ flux in future climate projections.

We produce a new estimate for global calcium carbonate production by coccolithophores using *in situ* measurements that is spatially, temporally, and depth resolved, providing new insights into regions of calcium carbonate production that have previously been overlooked. We use a machine learning model ensemble that predicts calcium carbonate production based on learned relationships between the *in situ* measurements and globally-resolved environmental predictors. Our model leverages the *in situ* measurements from Marsh et al. (2025), which provides expanded spatio-temporal coverage from Daniels et al. (2018). With our model we are able to explicitly resolve coccolithophore calcium carbonate production below the surface layer of the ocean without assuming an explicitly defined relationship with light that has been used for previous satellite estimates. To our knowledge, our estimate is the first globally integrated coccolithophore CP estimate derived directly from *in situ* measurements, rather than from basin-scale extrapolations or modeling CP from satellite remote sensing.

2 Methods

We determined the global patterns of calcium carbonate production (CP) by coccolithophores by interpolating sparse global CP observations using an ensemble of machine learning models. Compared with linear interpolation approaches, such as multiple linear regression (MLR), machine learning methods can capture non-linear relationships between the training and predictor data, thereby improving model performance in global ocean studies (Weber et al., 2019; Liu et al., 2021). Our model ensemble was trained to predict coccolithophore calcium carbonate production rates using the observational dataset of Marsh et al. (2025), together with globally depth-resolved monthly climatologies of environmental predictors. This approach allows us to reconstruct a globally depth-resolved monthly climatology of coccolithophore calcium carbonate production.

2.1 Calcium carbonate production data

The Marsh et al. (2025) dataset contains 3,160 observations of *in situ* measurements of CP rates ($\mu\text{mol C m}^{-3} \text{ d}^{-1}$) over a depth range of 0–193 m (Fig. 1). We implemented additional quality control steps. First, we only used measurements made using the ¹⁴C micro-diffusion technique (MDT), as this is the preferred method to measure CP and overcomes limitations of the other two methods (¹⁴C difference (Diff) and ⁴⁵Ca isotope) (remaining n = 2,922) (Daniels et al., 2018). Additionally, for data that included measurements of *G. huxleyi* cell counts (cells mL⁻¹), we removed observations where the estimated daily cell-specific calcium carbonate production exceeded a theoretical maximum for *G. huxleyi* ($\approx 3 \text{ pmol C cell}^{-1} \text{ d}^{-1}$, see discussions in Poulton et al. (2010) and Daniels et al. (2018), implemented here at a conservative $3.5 \text{ pmol C cell}^{-1} \text{ d}^{-1}$ cutoff).

The CP dataset was gridded onto a monthly, global 1-degree grid with 5-meter depth resolution for the top 200 meters to pair with the environmental predictor fields used for model training. For grid cells with multiple observations, we used the mean value. This gridding reduced the dataset to 1,896 observations. Observations without corresponding environmental data

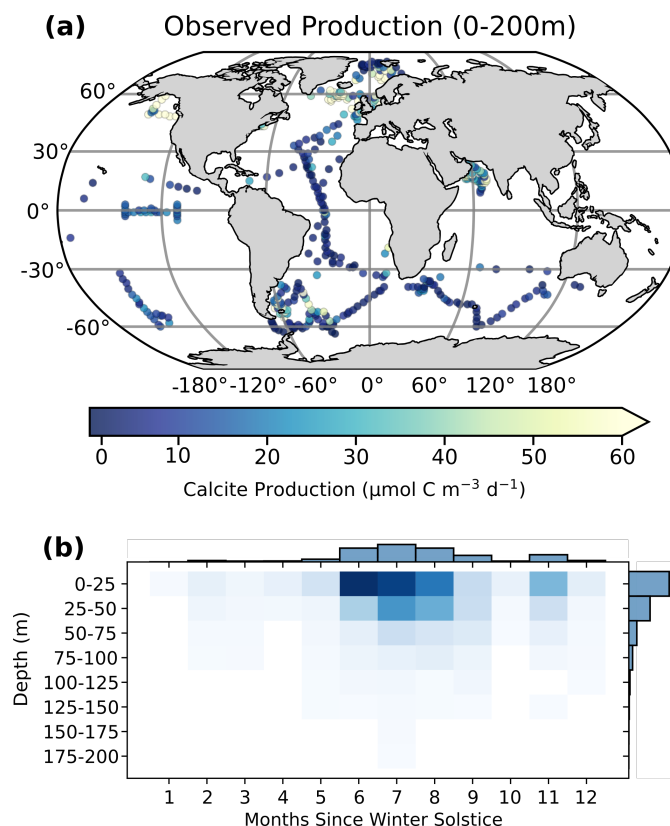


Figure 1. Global distribution of calcium carbonate production (CP) observations from Marsh et al. (2025). **(a)** Spatial distribution of CP rate measurements for the full depth domain (0-200 m). Units are in $\mu\text{mol C m}^{-3} \text{ d}^{-1}$. **(b)** Depth-time distribution of CP rate measurements. The time X-axis is shown as months since winter solstice to account for hemispheric differences in sampling seasons. The top X-axis and right Y-axis are histograms showing sample frequency.

were subsequently excluded, reducing the number of valid points to 1,858, indicating the limited environmental data coverage in high latitudes, marginal seas, and coastal regions.

125 A key limitation of the CP dataset is the lack of zero-value observations. This is due to inherent sampling bias as cruises that take these measurements are typically completed in seasons and regions where calcium carbonate production is expected (Daniels et al., 2018). Consequently, the predictive model is not explicitly trained to predict zero CP. This is a common problem in the field of species distribution modeling, where presences are recorded, but not absences (Barbet-Massin et al., 2012). To address this limitation, we introduced pseudo-zero observations within the dataset. While calcification has been observed
 130 under dark conditions in short-term incubation studies (see Paasche (2001) and references therein), the processes involved are energy intensive and must be sustained by respiration in the absence of light (Riebesell et al., 2000; Zondervan et al., 2001, 2002). We thereby assumed that CP by coccolithophores is close to zero when light is extremely limiting. We used a photosynthetically active radiation (PAR) database to identify depths where PAR falls below a very conservative threshold of



0.01% of the surface value. Pseudo-zero observations were then introduced below this depth using a 1:1 ratio of pseudo-zeros to observed CP values (Barbet-Massin et al., 2012). Barbet-Massin et al. (2012) recommend a ratio of 1:1 "pseudo-absences" to available "presences", in this case observed measurements of calcium carbonate production, with their locations informed by environmental conditions for machine-learning techniques in species distribution modeling. To evaluate this decision, we conducted ensemble runs with observations to pseudo-zero ratios ranging from 1:0 to 1:10, in increments of 1. We calculated summary statistics and total annual CP for each ensemble simulation. With increasing pseudo-zeros, the total annual CP decreases. At a ratio of 1:1, the total annual CP converged to an asymptote within the error range of a subsequent pseudo-zero addition, and thus was chosen.

2.2 Environmental predictors

We used a variety of physical, chemical and biological variables as environmental predictors for our model, including mixed-layer depth (MLD), temperature, nutrients (nitrate, phosphate, silicate), oxygen, carbonate chemistry (dissolved inorganic carbon and total alkalinity), and photosynthetically active radiation (PAR). These predictors were chosen as they relate to nutrient and light supply for photosynthesis and carbonate chemistry, which impacts the kinetics of calcification, or represent competition with other marine phytoplankton (in the case of silicate for diatoms) (Zondervan, 2007; Durak et al., 2016). All predictors were regridded onto the same 1-degree, 0–200 m, monthly grid used for CP observations using the xESMF conservative interpolation algorithm (Zhuang et al., 2023). For non-depth resolved variables such as MLD, surface values were repeated for each depth level.

MLD comes from the Mixed Layer Depth Climatology dataset, compiled from the ARGO program and the NCEI-NOAA World Ocean Database (de Boyer Montégut, 2023; de Boyer Montégut et al., 2004). Temperature, oxygen, and nutrients come from the World Ocean Atlas 2018 (Locarnini et al., 2018; Garcia et al., 2019b, a), while dissolved inorganic carbon (DIC) and total alkalinity (TA) come from NNGv2 (Broullón et al., 2020). PAR comes from a depth-resolved gridded climatology, where missing remote sensing values were filled using the Environmental String Model (Castant et al., 2024).

We explored using remote sensing predictors from the Aqua MODIS sensor, specifically the reflectance bands Rrs_547 and Rrs_667, which are used to derive particulate inorganic carbon concentrations (Mitchell et al., 2017), and the derived chlorophyll-*a* product (NASA Ocean Biology Processing Group, 2022a, b). However, we found that including these predictors made the model too sensitive to artifacts in shallow regions leading to single pixel anomalous values and did not substantially improve overall model performance. We thus decided to omit them from the final model predictors.

2.3 Machine learning ensemble

To predict calcium carbonate production, we used the Aquatic Biogeochemical Interpolation Library (ABIL.PY), an ensemble of machine learning algorithms as implemented in de Vries et al. (2025c). The models used in the ensemble consist of Extreme Gradient Boosting (XGB), bagged K-Nearest Neighbors (bKNN), and Random Forests (RF), the last two from SCIKIT-LEARN (Chen and Guestrin, 2016; Pedregosa et al., 2011). The models are trained using paired CP observations and their local predictors, and then projected back onto the fully resolved predictor grid. To avoid overfitting, we applied 10-fold cross-validation,



where 90% of the data was used for training and 10% for validation, repeated 10 times over the entire dataset. The hyperparameters for each model were optimized using GRIDSEARCHCV to maximize R^2 . The optimized parameters are reported in Appendix A (Add). Model performance was assessed with and without log transformation of the CP data during training, with the log-transformed model performing better, and therefore adopted for the final prediction.

2.4 Model performance

The ensemble validation (out-of-sample) R^2 was 0.352, the relative root mean square error (RMSE) was 1.02, and the relative mean absolute error (MAE) was 0.158. For the complete dataset, the logged ensemble output vs. observed values R^2 was 0.93, the r was 0.99, the RMSE was $105.7 \mu\text{mol C m}^{-3} \text{ d}^{-1}$ and the mean residual was $10.7 \mu\text{mol C m}^{-3} \text{ d}^{-1}$ (Fig. S1).

2.5 Uncertainty quantification

To estimate ensemble uncertainty, individual predictions within each model (RF, bKNN, and XGB) were used to infer 95th percentile confidence intervals. This an inherent capability for RF (decision trees) and bKNN (bags), but not XGB, which we rectified by adding a bagging step. This provides us with an uncertainty quantification for each model, which we then combine to calculate the 95th percentiles using loss-weighted quantiles (de Vries et al., 2025c).

2.6 Superbiomes

For regional analysis, we used the Fay and McKinley (2014) mean biomes, which provide 17 physical, biologically defined regions, separated by ocean basin. These biomes were derived from their sea ice fraction, sea surface temperature, chlorophyll- a concentration, and maximum mixed-layer depth. To support our interpretation of the results, we merged these regions into 5 superbiomes: 'ice', 'subpolar seasonally stratified', 'subtropical seasonally stratified', 'subtropical permanently stratified', and 'equatorial'.

For each superbiome, we calculated the percentage contribution to the globally integrated total CP using sample reconstruction with the 95th percentile predictions. We used the percent contribution for each biome from the 2.5 and 97.5 percentile predictions to approximate gamma distributions, and then sampled 10,000 values within that distribution to then estimate the mean, standard deviation and 95th percentile range for each biome's contribution to the global integrated CP. The same was done with each biome's mean annual CP (for the 2.5 and 97.5 percentile predictions) and mean cellular inorganic carbon content (from de Vries et al. (2025b, a)), to determine biome-specific turnover rates. This method was also used for the euphotic zone estimates, where each zone, as defined through floral analysis by Poulton et al. (2017), upper euphotic (10–100% surface irradiance), lower euphotic (1–10% surface irradiance), and sub-euphotic (< 1% surface irradiance) was treated as a "biome."

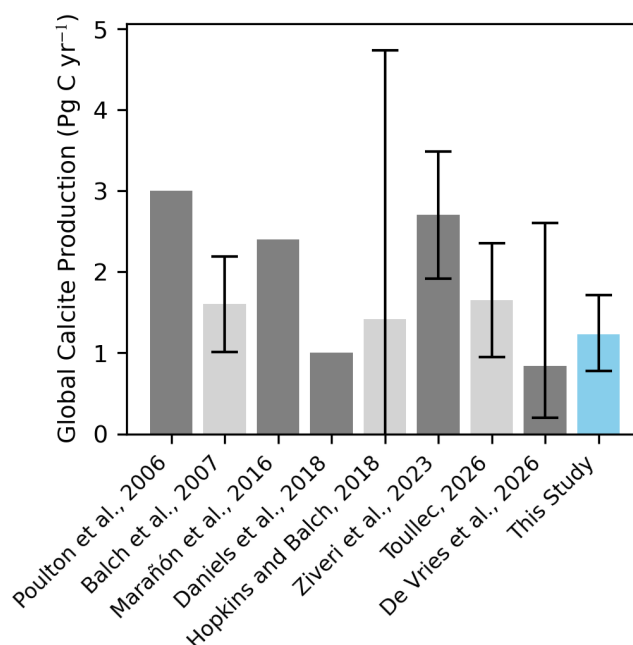


Figure 2. Estimates of global calcium carbonate production by coccolithophores (Pg C yr^{-1}). Previous estimates include satellite-based algorithms (light gray) (Balch et al., 2007; Hopkins and Balch, 2018; Toullec, 2026) and extrapolations from *in situ* measurements (dark gray) (Poulton et al., 2006; Marañón et al., 2016; Daniels et al., 2018; Ziveri et al., 2023; de Vries et al., 2025b). Note that each method's estimate's error bars are calculated differently and are therefore not inherently comparable. Estimates with standard deviations were converted to 95% confidence intervals.

3 Results and discussion

195 3.1 Global integrated calcium carbonate production by coccolithophores

Our model predicts a global annual calcium carbonate production (CP) by coccolithophores of $1.23 \text{ Pg C yr}^{-1}$ [0.78, 1.71], consistent with previous estimates derived from extrapolated sparse datasets and satellite products ($1.0\text{--}3.0 \text{ Pg C yr}^{-1}$, Fig. 2). Estimates from Balch et al. (2007), Hopkins and Balch (2018), Toullec (2026) are derived from satellite-based algorithms, while those from Poulton et al. (2006), Marañón et al. (2016), Daniels et al. (2018), Ziveri et al. (2023), and de Vries et al. (2025b) rely on sparse *in situ* measurements of calcium carbonate stocks or production rates, extrapolated globally.

200 3.2 Regional and seasonal surface distributions

Looking first at surface rates, our model predicts strong spatial and seasonal variability in surface calcium carbonate production (CP) as expected, with peak rates ($>60 \mu\text{mol C m}^{-3} \text{ d}^{-1}$) in the high latitudes during MAM (March, April, May) and JJA (June, July, August) in the Icelandic Basin and Gulf Stream in the North Atlantic as well as in the Gulf of Alaska in the



205 North Pacific (Fig. 3a–d). Production then shifts to the Southern Ocean during SON (September, October, November) and DJF
 (December, January, February), with particularly high rates along the Patagonian shelf and throughout the Great Calcite Belt, a
 region of high particulate inorganic carbon concentrations around the Southern Ocean previously observed via satellites (Balch
 et al., 2005). Upwelling regions in the Equatorial Pacific, Arabian Sea, Bay of Bengal, and Atlantic eastern boundary currents
 sustain year-round moderate production ($\approx 30 \mu\text{mol C m}^{-3} \text{ d}^{-1}$). The subtropical gyres and Arctic and Southern Oceans have
 210 relatively low year-round production ($< 15 \mu\text{mol C m}^{-3} \text{ d}^{-1}$).

3.3 Depth distributions

Below the surface, calcium carbonate production decreases with depth. Overall, zonal mean annual production is highest at the
 surface and decreases with depth (Fig. 3e). The highest zonal mean CP values are found at the surface in the northern high lati-
 tudes ($40\text{--}60^\circ\text{N}$) ($> 30 \mu\text{mol C m}^{-3} \text{ d}^{-1}$), dropping below $2.5 \mu\text{mol C m}^{-3} \text{ d}^{-1}$ by 75 m. Production is $> 15 \mu\text{mol C m}^{-3} \text{ d}^{-1}$ in
 215 the Equatorial region ($10^\circ\text{S} - 10^\circ\text{N}$) and the Great Calcite Belt (45°S), dropping below $2.5 \mu\text{mol C m}^{-3} \text{ d}^{-1}$ by 105 m and 80 m,
 respectively. In contrast, the subtropical gyres (25°N/S) have rates near $10 \mu\text{mol C m}^{-3} \text{ d}^{-1}$ in the surface that remains above
 $2.5 \mu\text{mol C m}^{-3} \text{ d}^{-1}$ until around 150 m, persisting more than 25 m below the euphotic zone.

The attenuation of CP with depth can be viewed spatially as well (Fig. 3f). Consistent with the zonal mean patterns, CP
 attenuates rapidly with depth in the high latitudes and equatorial regions, reaching $< 1\%$ of its surface values by 100 m or
 220 shallower. In the subtropical gyres, however, attenuation is weaker, with $> 1\%$ surface production persisting throughout the
 top 200 m. As such, regions that are highly productive tend to attenuate faster with depth, while regions of lower production
 attenuate slower with depth.

3.4 Seasonal variability by superbiome

Calcium carbonate production varies strongly throughout the year. The strong seasonality at high latitudes is reflected in
 225 the monthly superbiome mean upper euphotic zone CP rates (Fig. 4). The strongest seasonality is seen in the subpolar (SP)
 superbiome, where the difference between the summer maximum and winter minimum CP is $16.1 \mu\text{mol C m}^{-3} \text{ d}^{-1}$. This is
 followed by the subtropical seasonally stratified (STSS) superbiome, with a range of $10.2 \mu\text{mol C m}^{-3} \text{ d}^{-1}$, and the ice-covered
 (ICE) superbiome, with a range of $\approx 4.2 \mu\text{mol C m}^{-3} \text{ d}^{-1}$. The subtropical permanently stratified (STPS) and equatorial
 (EQU) superbiomes are less seasonal, with ranges of $1.8 \mu\text{mol C m}^{-3} \text{ d}^{-1}$ and $1.2 \mu\text{mol C m}^{-3} \text{ d}^{-1}$, respectively.

230 3.5 Subtropical regions dominate global coccolithophore calcium carbonate production

Due to deeper production and lower seasonality in the low latitudes, the highest depth-integrated production rates occur in the
 subpolar North Pacific, subpolar North Atlantic, and subtropical South Pacific gyres, exceeding $500 \text{ mmol C m}^{-2} \text{ yr}^{-1}$ (Fig. 5a).
 The Great Calcite Belt is not as strongly present as in the surface fields, with only small areas exceeding $300 \text{ mmol C m}^{-2} \text{ yr}^{-1}$ off
 the southwest coast of South America and the southwest coast of Australia.

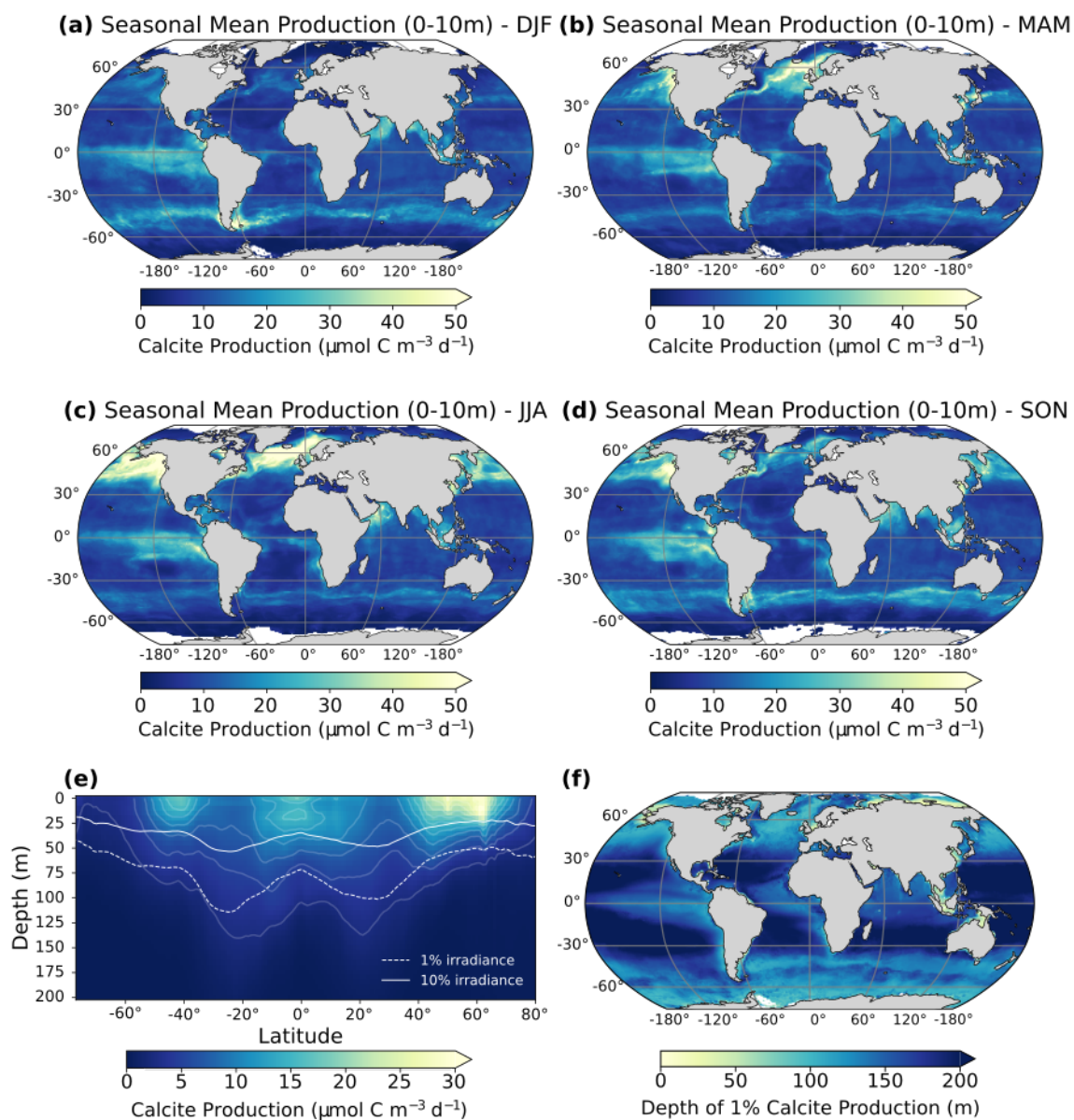


Figure 3. Coccolithophore calcium carbonate production (CP) predicted by machine learning ensemble. Panels **(a, b, c, d)** show surface seasonal mean CP (0–10 m; $\mu\text{mol C m}^{-3} \text{ d}^{-1}$). Panel **(e)** shows zonal mean calcite production, with contours at $2.5 \mu\text{mol C m}^{-3} \text{ d}^{-1}$ and overlaid solid white and dashed white lines showing the depth where PAR reaches 10% surface irradiance and 1% surface irradiance, respectively. Panel **(f)** shows the depth at which calcite production reaches 1% of the surface value.

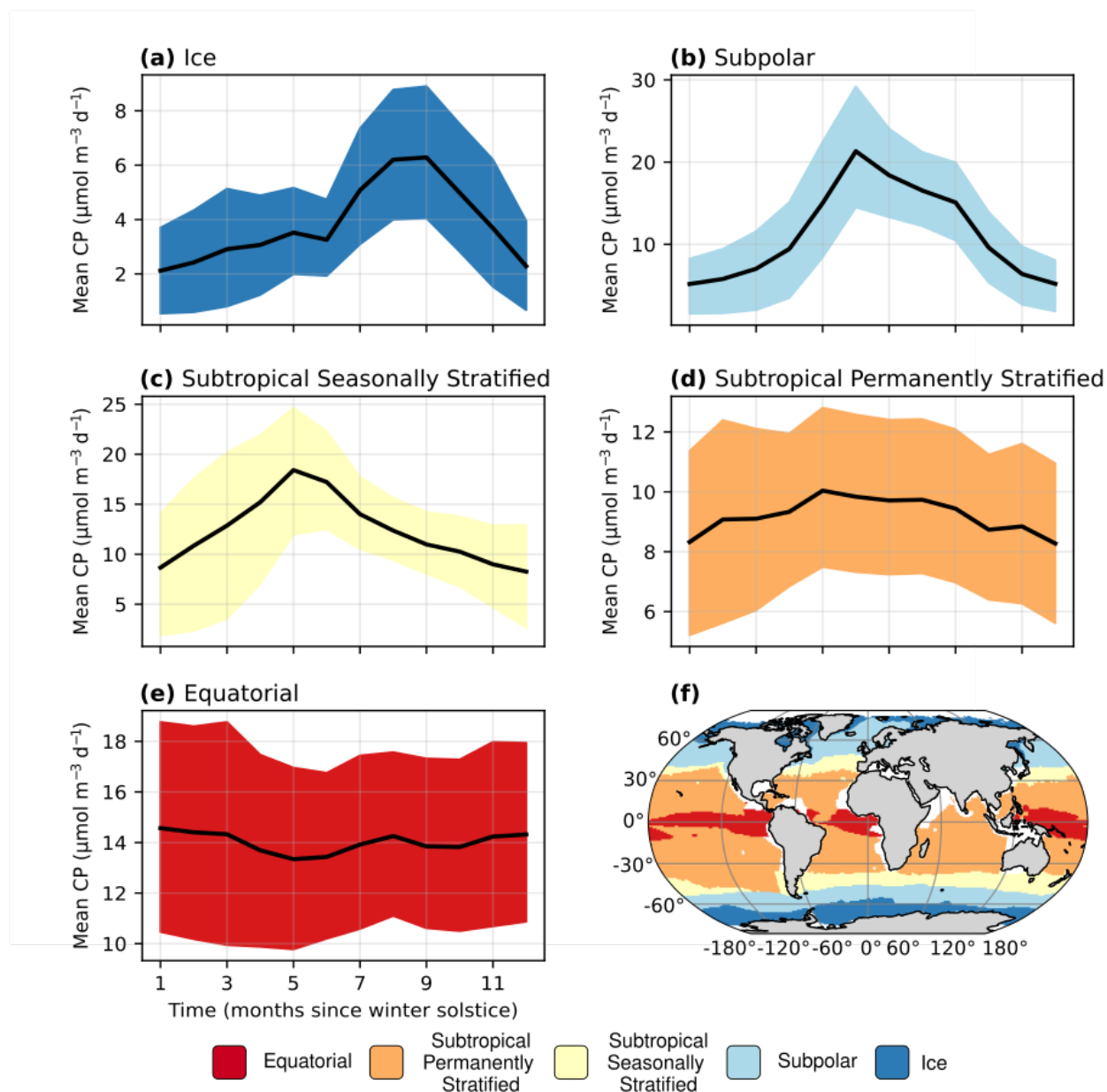


Figure 4. Monthly mean calcium carbonate production rates by biome for the upper euphotic zone ($>10\%$ surface irradiance). Hemispheres have been joined by months since winter solstice. Biomes are adapted from Fay and McKinley (2014). Units are in $\mu\text{mol C m}^{-3} \text{d}^{-1}$.



235 Within the upper euphotic zone, the equatorial (EQU) superbiorne has the highest mean rate ($13.7 \mu\text{mol C m}^{-3} \text{d}^{-1}$ [9.8, 18.6]), followed by the subtropical seasonally stratified (STSS) superbiorne ($11.3 \mu\text{mol C m}^{-3} \text{d}^{-1}$ [6.1, 18.7]) and the subpolar (SP) and subtropical permanently stratified (STPS) superbiornes ($10.4 \mu\text{mol C m}^{-3} \text{d}^{-1}$ [5.6, 17.2] and $9.0 \mu\text{mol C m}^{-3} \text{d}^{-1}$ [6.2, 12.7], respectively) (Fig. 5b). While the SP superbiorne has the highest seasonal productivity ($21.3 \mu\text{mol C m}^{-3} \text{d}^{-1}$ [14.5, 29.2] in summer), its strong seasonality results in lower mean annual integrated production ($5.5 \mu\text{mol C m}^{-3} \text{d}^{-1}$ [0.29, 15.1]) compared to the more weakly seasonal STPS, STSS and EQU superbiornes, leading to higher mean rates in these biomes ($5.2 \mu\text{mol C m}^{-3} \text{d}^{-1}$ [1.0, 11.6], $5.5 \mu\text{mol C m}^{-3} \text{d}^{-1}$ [0.4, 16.5], and $7.2 \mu\text{mol C m}^{-3} \text{d}^{-1}$ [0.8, 17.2], respectively, Figs. 4, 5b). When integrated over their volume and for the entire year, the STPS superbiorne dominates global CP, contributing 59.0% [46.0, 70.3] of the total (with 29.2% [21.5, 37.6], 17.5% [11.9, 24.4], 12.1% [6.7, 19.1] from the Upper, Lower, and Sub Euphotic Zones, respectively). The SP, EQU, and STSS regions each contribute about 12-14% globally (Fig. 5c).

245 3.6 Differences in resolving calcite production with depth compared to satellites

A key advantage of our model is its ability to explicitly predict production at depths up to 200 m, rather than relying on an assumed exponential decay profile as is commonly done in satellite-based estimates, where the depth resolution is restricted to the first optical depth (< 40 m) (Hopkins and Balch, 2018). To directly compare these approaches, we prescribed CP using our model surface calcium carbonate production (depth = 0 m), restricted to the domain of the monthly climatology of the diffuse 250 attenuation of light at 490 nm (K_d490), and then calculated the production at depth for each level following Hopkins and Balch (2018) (Figure 6a). The global mean vertical profile shows that assuming decay with K_d490 results in a rapid production decline with depth, reaching values $< 1 \mu\text{mol C m}^{-3} \text{d}^{-1}$ by 75 m, compared to 135 m for our model. These differences in vertical attenuation vary spatially (Fig. 6b). Overall, our model predicts a deeper global depth at which CP reaches 1% of its surface value compared to the K_d490 -based decay used in Hopkins and Balch (2018), with the largest differences in coastal 255 regions, upwelling regions, and the high latitudes (Fig. 6b). Assuming a K_d490 attenuation results in a 61% lower estimate of global annual calcium carbonate production ($0.48 \text{ Pg C yr}^{-1}$ vs. $1.24 \text{ Pg C yr}^{-1}$), highlighting the importance of explicitly resolving calcium carbonate production with depth.

3.6.1 Calcium carbonate production in the sub euphotic zone

We predict 18.4% [9.2, 30.8] of the global annual CP occurs below the euphotic zone ($\text{PAR} < 1\%$). Median CP rates are 260 much lower here ($1.08 \mu\text{mol C m}^{-3} \text{d}^{-1}$ [0.5, 2.0]). The sub euphotic zone is often occupied by low-light adapted species such as *F. profunda* and *G. flabellatus*, which have been observed at depths below 1% and even deeper than 0.1% surface PAR (Poulton et al., 2017). For *F. profunda* in particular, their distributions are found primarily in the subtropical and tropical regions, where they maintain inorganic carbon stocks year-round with little seasonality, while also comprising 6.7% [2.3, 13.2] of the global cellular PIC stock, similar to that of *G. huxleyi* (7%) (de Vries et al., 2025b). *F. profunda* is heavily calcified, with 265 a median cellular PIC:POC ratio (mol mol^{-1}) of 4.86 [4.82, 4.9] (de Vries et al., 2024). These sub euphotic zone species may be mixotrophic, potentially supporting their growth and calcification costs via ingestion of bacteria, small picoplankton and/or

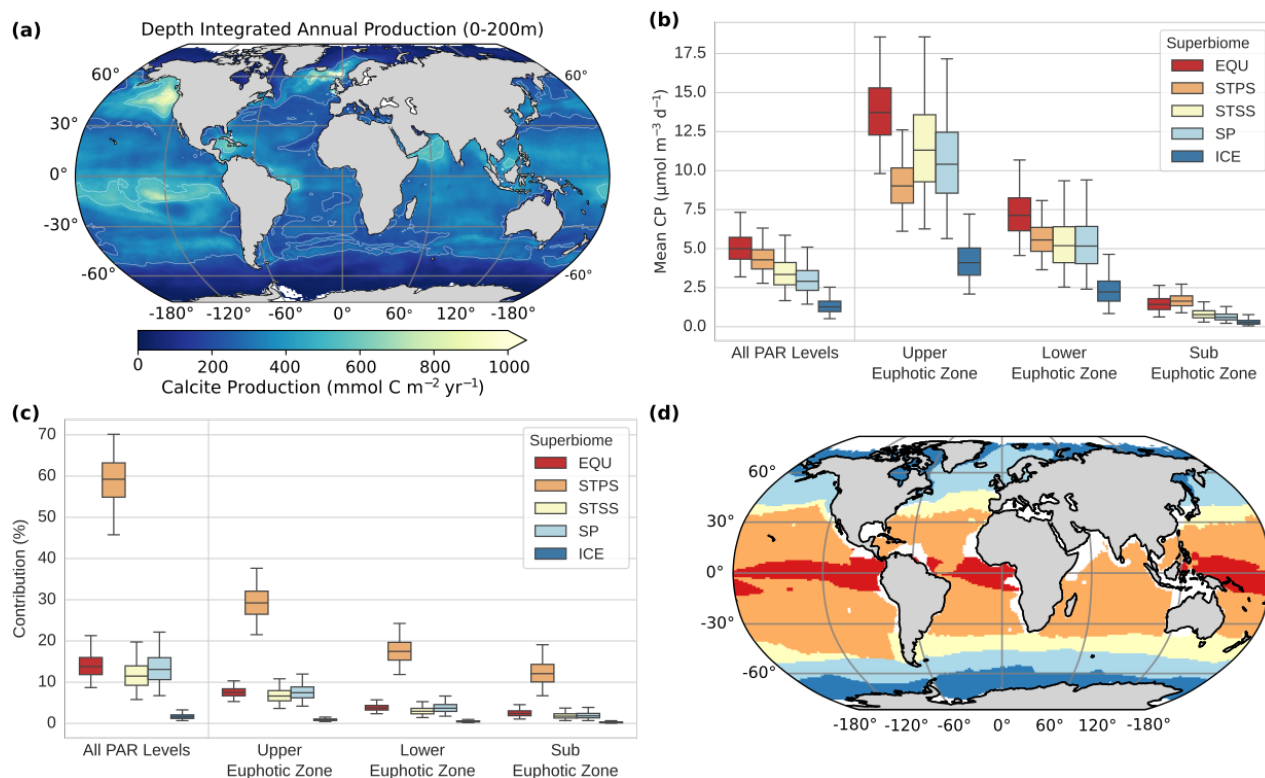


Figure 5. Coccolithophore depth-integrated annual calcium carbonate production (CP) predicted by the machine learning ensemble. **(a)** Annual depth-integrated CP (0-200 m; $\text{mmol C m}^{-2} \text{yr}^{-1}$). Contour line shows 250 $\text{mmol C m}^{-2} \text{yr}^{-1}$ intervals. **(b)** Spatiotemporal mean CP by photic zone and superbiome. **(c)** Percent contribution of each photic zone and superbiome to global integrated annual CP. **(d)** Distribution of the superbiomes adapted from Fay and McKinley (2014). Global spatiotemporal mean and integrated contributions for each superbiome for all PAR values are shown, followed by the photic zones, which are derived from PAR, where PAR > 10 % of the surface is the Upper Euphotic Zone, 10 % > PAR > 1 % of the surface is the Lower Euphotic Zone, and PAR < 1 % of the surface is the Sub Euphotic Zone (Poulton et al., 2017).

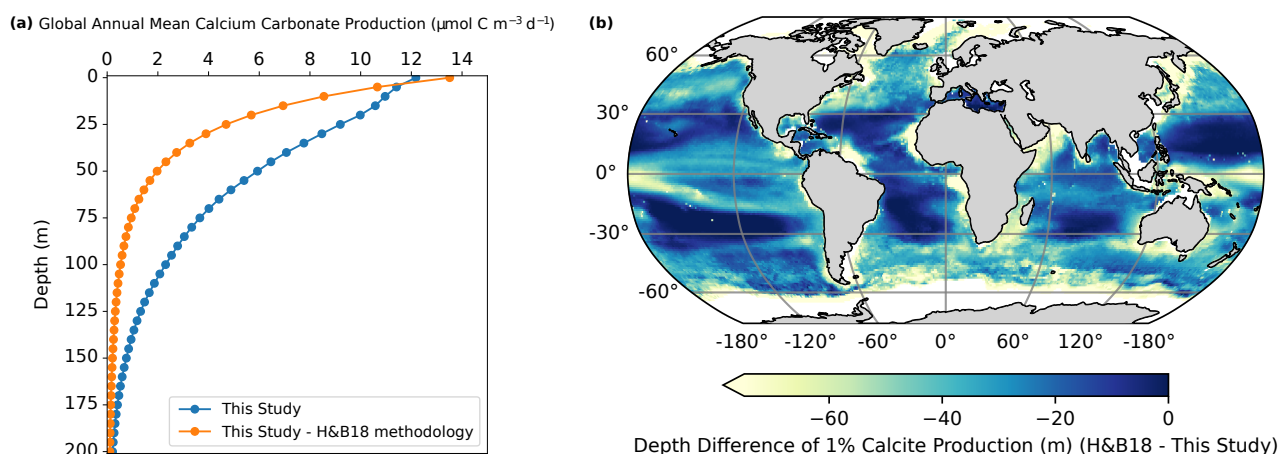


Figure 6. Comparison of calcium carbonate production (CP) depth profiles between depth-resolved machine learning product and prescribed satellite-based decay. **(a)** Mean global CP at each depth level for our model (blue), and how the model would predict using Hopkins and Balch (2018) methodology. The difference in surface values reflects the exclusion of lower values in the high latitudes which are lost when the surface prediction is restricted to the satellite domain, leading to a higher mean value at the surface for the H&B methodology. **(b)** Spatial difference in the depth at which CP reaches 1% of its surface value for our model compared to following the Hopkins and Balch (2018) methodology. Negative values indicate that the Hopkins and Balch (2018) 1% depth is shallower than our fully depth-resolved model.

dissolved organic matter (Poulton et al., 2017). By maintaining their heavily calcified shells year-round, these species could potentially contribute substantially to global annual CP and inorganic carbon export.

3.7 Coccolithophore inorganic carbon turnover rate

The turnover rate is the frequency at which calcium carbonate is replaced per unit time (or the inverse of turnover time), where a higher value indicates faster cycling. We calculated calcium carbonate turnover rates for each euphotic region within the superbiomes by combining our calcium carbonate production fields with coccolithophore inorganic carbon stocks derived from de Vries et al. (2025b) (Fig. 7). de Vries et al. (2025b) applied a similar machine learning approach to predict total living cell-specific inorganic carbon content associated with living coccolithophore species. Resulting global median turnover rates range from 0.21 to 1.00 d^{-1} , comparable to previous estimates of total (not living cell-specific) PIC turnover rates using *in situ* data (0.02-0.4 d^{-1}) (Poulton et al., 2006; Marañón et al., 2016) as well as coccolithophore cell-normalized growth rates (0.42 - 1.4 d^{-1}) (Krumhardt et al., 2019). Interestingly, based on superbiome trends, mean inorganic carbon stocks (C_{IC}) (Fig. 7a) are highest in the subtropical seasonally stratified and subpolar superbiomes, while CP is highest in the equatorial and subtropical permanently stratified superbiomes (Fig. 5b). As a result, turnover rate follows the same pattern as CP, with the highest turnover rates in the equatorial superbiome, declining poleward with each subsequent superbiome. Across all superbiomes, turnover rate decreases with depth through the euphotic zone. However, turnover rates in the EQU superbiome remain high even in the Sub

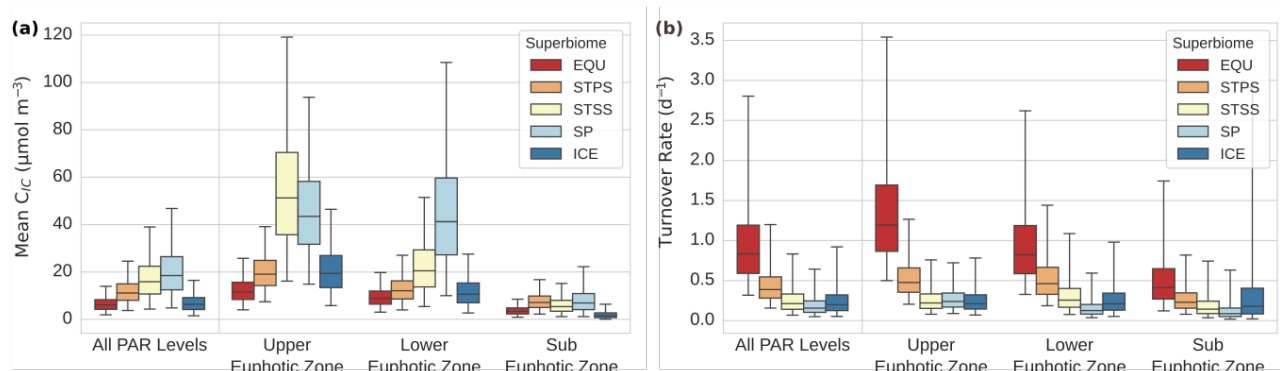


Figure 7. (a) Coccolithophore inorganic carbon stock from de Vries et al. (2025a) and (b) calcium carbonate turnover rates for each photic region and superbiome based on Fay and McKinley (2014). Global spatiotemporal mean and turnover rates for each superbiome for all PAR values are shown, followed by the photic zones, which are derived from PAR, where PAR > 10 % of the surface is the Upper Euphotic Zone, 10 % > PAR > 1 % of the surface is the Lower Euphotic Zone, and PAR < 1 % of the surface is the Sub Euphotic Zone. Turnover rates are derived using the biome mean calcium carbonate production from this study (Fig. 5b) and the biome mean coccolithophore inorganic carbon stock from de Vries et al. (2025b).

Euphotic Zone, with a median turnover rate of 0.55 d^{-1} , more than double the Upper Euphotic Zone turnover rates for the STSS, SP, and ICE superbiomes (0.22 , 0.24 , and 0.21 d^{-1} respectively).

Many studies have used coccolithophore turnover times (0.7 - 10 d , 0.1 - $1.5 \text{ cell divisions d}^{-1}$) (Krumhardt et al., 2019; Ziveri et al., 2023; Han et al., 2025) to derive calcification rates from coccolithophore standing stocks, assuming that coccolithophore growth rate is equal to the calcium carbonate turnover rate. This leverages the assumption that PIC/POC ratios are stable over the the growth cycle, which is often unstated. However, PIC/POC ratios are not static, and vary during the growth cycle (Kottmeier et al., 2020). Globally, PIC/POC ratios (specifically coccolithophore cellular carbon instead of particulate carbon that often includes detached coccoliths) are spatially heterogeneous, with elevated ratios (> 1.5) in subpolar and deep subtropical regions associated with heavily calcified species such as *C. pelagicus* and *F. profunda*, respectively, with lower PIC/POC elsewhere (de Vries et al., 2025b). This heterogeneity is often overlooked in climate models as well (Planchat et al., 2023). By modeling CP directly from *in situ* measurements, we can capture spatiotemporal variability in production that conversion from inorganic stocks and growth rates cannot.

3.8 Uncertainties and future directions

Our model depends on the availability of *in situ* measurements of calcite production. The observational data is biased towards the surface regions and therefore deeper regions may be poorly constrained. The distribution of CP with depth plays a large part in which regions end up contributing the most to global CP, particularly in the subtropical gyres, and therefore should be further



explored with observational data considering how important these regions are for global CP. In particular, the decoupling of photosynthesis and calcification by coccolithophores spatially and temporally are of unique interest.

300 Two particular regions that highlight the need for additional field based observations are the Indo-Pacific and North Pacific Gyre. The Indo-Pacific, in particular the South China Sea and Bay of Bengal, appear to be regions of potentially high CP, but have no observations. Additionally much of the North Pacific and South Pacific Gyre regions are lacking in observations, yet are predicted to be the two highest contributing biomes to global CP. Predicting these regions is within the model domain as they may have similar conditions to other sampled regions. However, they may be processes affecting local CP rates that are
305 not captured by our environmental data domain, and so it would be useful to validate these highly productive regions with *in situ* measurements.

4 Conclusions

Here we present the first global, depth-resolved estimate of monthly calcium carbonate production by coccolithophores for the top 200 m of the ocean. Our model leverages *in situ* measurements of these rates with well constrained global climatologies
310 of environmental data to predict each grid cell individually, allowing us to predict production at depth without explicitly prescribing a parametric relationship to extrapolate from surface measurements. We calculate a global annual coccolithophore calcium carbonate production of $1.23 \text{ Pg C yr}^{-1}$ [0.78, 1.71]. While high-latitude regions show strong seasonal blooms, the low-latitude subtropical permanently stratified superbiome accounts for the vast majority (59%) of global annual integrated CP due to its annual consistency with low seasonality and deeper production. Explicitly resolving production with depth
315 reveals that 18.4% of global CP occurs below the euphotic zone ($\text{PAR} < 1\%$) and demonstrates that satellite approaches assuming a $K_d(490)$ -based vertical decay underestimate annual global production by over 60%. Satellite estimates do however, provide much higher temporal and spatial resolution (daily, 4 km resolution for MODIS-AQUA particulate organic carbon) for the surface ocean that our model does not. By explicitly predicting production at depth, our model can be leveraged alongside satellites estimates to provide valuable information for marine biogeochemical models in terms of the spatiotemporal
320 distributions of calcium carbonate production.



Code and data availability. Abil can be found at <https://github.com/nanophyto/Abil> and installed via pip. The specific scripts used to produce the results from this paper can be found at https://github.com/nicola-wiseman/Abil_Wiseman2025. Environmental data for model training can be found at <https://zenodo.org/records/16753618>. The calcification dataset can be found at <https://doi.org/10.1594/PANGAEA.987673>. Modeled calcium carbonate production output can be found at <https://zenodo.org/records/23241589>.

325 *Author contributions.* FMM, JdV and NAW designed the study. JdV, LJW and NAW developed the model. NJM and AJP provided observational data. NAW performed the model simulations and analyzed the results. NAW wrote the manuscript. All authors commented on the manuscript.

Competing interests. The authors declare no competing interests.

Acknowledgements. We thank the scientists and cruises that collected the calcification data. We also thank the participants of the Advances in
330 Coccolithophore Research meeting for their comments, feedback, and support. This work was carried out using the computational facilities of the Advanced Computing Research Centre, University of Bristol - <http://www.bristol.ac.uk/acrc/>. This work was supported by funding from the UK Research and Innovation Natural Environment Research Council grant CoccoTrait, NE/X001261/1 (FMM, JdV, AJP, LJW).



References

- Archer, D., Kheshgi, H., and Maier-Reimer, E.: Dynamics of fossil fuel CO₂ neutralization by marine CaCO₃, *Global Biogeochemical Cycles*, 12, 259–276, <https://doi.org/10.1029/98GB00744>, 1998.
- Balch, W., Drapeau, D., Bowler, B., and Booth, E.: Prediction of pelagic calcification rates using satellite measurements, *Deep Sea Research Part II: Topical Studies in Oceanography*, 54, 478–495, 2007.
- Balch, W. M. and Mitchell, C.: Remote sensing algorithms for particulate inorganic carbon (PIC) and the global cycle of PIC, *Earth-Science Reviews*, 239, 104363, <https://doi.org/10.1016/j.earscirev.2023.104363>, 2023.
- 340 Balch, W. M., Gordon, H. R., Bowler, B. C., Drapeau, D. T., and Booth, E. S.: Calcium carbonate measurements in the surface global ocean based on Moderate-Resolution Imaging Spectroradiometer data, *Journal of Geophysical Research: Oceans*, 110, <https://doi.org/10.1029/2004JC002560>, 2005.
- Barbet-Massin, M., Jiguet, F., Albert, C. H., and Thuiller, W.: Selecting pseudo-absences for species distribution models: how, where and how many?, *Methods in Ecology and Evolution*, 3, 327–338, <https://doi.org/10.1111/j.2041-210X.2011.00172.x>, 2012.
- 345 Beaufort, L., Probert, I., de Garidel-Thoron, T., Bendif, E. M., Ruiz-Pino, D., Metzl, N., and de Vargas, C.: Sensitivity of coccolithophores to carbonate chemistry and ocean acidification, *Nature*, 476, 80–83, <https://doi.org/10.1038/nature10295>, 2011.
- Behrenfeld, M. J., Boss, E., Siegel, D. A., and Shea, D. M.: Carbon-based ocean productivity and phytoplankton physiology from space, *Global Biogeochemical Cycles*, 19, <https://doi.org/10.1029/2004GB002299>, 2005.
- Berelson, W. M., Balch, W. M., Najjar, R., Feely, R. A., Sabine, C., and Lee, K.: Relating estimates of CaCO₃ production, export, and
 350 dissolution in the water column to measurements of CaCO₃ rain into sediment traps and dissolution on the sea floor: A revised global carbonate budget, *Global Biogeochemical Cycles*, 21, <https://doi.org/10.1029/2006GB002803>, 2007.
- Broecker, W. S. and Takahashi, T.: Neutralization of Fossil Fuel CO₂ by Marine Calcium Carbonate, in: *The Fate of Fossil CO₂ In The Oceans*, edited by Anderson, N. R. and Malahoff, A., pp. 213–239, Plenum Press, New York, 1977.
- Broullón, D., Pérez, F. F., Velo, A., Hoppema, M., Olsen, A., Takahashi, T., Key, R. M., Tanhua, T., Santana-Casiano, J. M., and Kozyr, A.:
 355 A global monthly climatology of oceanic total dissolved inorganic carbon: a neural network approach, *Earth System Science Data*, 12, 1725–1743, <https://doi.org/10.5194/essd-12-1725-2020>, 2020.
- Castant, J., Vantrepotte, V., Frouin, R., and Beaugrand, G.: Comprehensive gridded dataset of photosynthetically active radiation in the upper ocean from 1958 to 2022, *Remote Sensing of Environment*, 311, 114305, <https://doi.org/10.1016/j.rse.2024.114305>, 2024.
- Chen, T. and Guestrin, C.: XGBoost: A Scalable Tree Boosting System, in: *Proceedings of the 22nd ACM SIGKDD International Conference on Knowledge Discovery and Data Mining, KDD '16*, p. 785–794, Association for Computing Machinery, New York, NY, USA, ISBN 9781450342322, <https://doi.org/10.1145/2939672.2939785>, 2016.
- 360 Daniels, C. J., Poulton, A. J., Balch, W. M., Marañón, E., Adey, T., Bowler, B. C., Cermeño, P., Charalampopoulou, A., Crawford, D. W., Drapeau, D., Feng, Y., Fernández, A., Fernández, E., Fragos, G. M., González, N., Graziano, L. M., Heslop, R., Holligan, P. M., Hopkins, J., Huete-Ortega, M., Hutchins, D. A., Lam, P. J., Lipsen, M. S., López-Sandoval, D. C., Loucaides, S., Marchetti, A., Mayers, K. M. J., Rees, A. P., Sobrino, C., Tynan, E., and Tyrrell, T.: A Global Compilation of Coccolithophore Calcification Rates, *Earth System Science Data*, 10, 1859–1876, <https://doi.org/10.5194/essd-10-1859-2018>, 2018.
- de Boyer Montégut, C.: Mixed layer depth climatology computed with a density threshold criterion of 0.03kg/m³ from 10 m depth value, <https://doi.org/10.17882/91774>, 2023.



- de Boyer Montégut, C., Madec, G., Fischer, A. S., Lazar, A., and Iudicone, D.: Mixed layer depth over the global ocean: An examination of
370 profile data and a profile-based climatology, *Journal of Geophysical Research: Oceans*, 109, <https://doi.org/10.1029/2004JC002378>, 2004.
- de Vries, J., Poulton, A. J., Young, J. R., Monteiro, F. M., Sheward, R. M., Johnson, R., Hagino, K., Ziveri, P., and Wolf, L. J.: CASCADE:
Dataset of extant coccolithophore size, carbon content and global distribution, *Scientific data*, 11, 920, 2024.
- de Vries, J., Monteiro, F., Poulton, A., Wiseman, N., and Wolf, L.: Modelled coccolithophore inorganic carbon dataset,
<https://doi.org/10.5281/zenodo.16887386>, 2025a.
- 375 de Vries, J., Monteiro, F. M., Poulton, A. J., Wiseman, N. A., and Wolf, L. J.: A diverse community constitutes global coccolithophore
calcium carbonate stocks, *bioRxiv*, <https://doi.org/10.1101/2025.09.11.675535>, 2025b.
- de Vries, J., Wiseman, N. A., and Wolf, L. J.: Abil: A Python package for the interpolation of aquatic biogeochemical datasets, *Journal of
Open Source Software*, 10, 8755, <https://doi.org/10.21105/joss.08755>, 2025c.
- DeVries, T. and Primeau, F.: Dynamically and Observationally Constrained Estimates of Water-Mass Distributions and Ages in the Global
380 Ocean, *Journal of Physical Oceanography*, 41, 2381–2401, <https://doi.org/10.1175/JPO-D-10-05011.1>, 2011.
- Durak, G. M., Taylor, A. R., Walker, C. E., Probert, I., de Vargas, C., Audic, S., Schroeder, D., Brownlee, C., and Wheeler, G. L.: A role for
diatom-like silicon transporters in calcifying coccolithophores, *Nature Communications*, 7, 10 543, <https://doi.org/10.1038/ncomms10543>,
2016.
- Fay, A. R. and McKinley, G. A.: Global open-ocean biomes: mean and temporal variability, *Earth System Science Data*, 6, 273–284,
385 <https://doi.org/10.5194/essd-6-273-2014>, 2014.
- Field, C. B., Behrenfeld, M. J., Randerson, J. T., and Falkowski, P.: Primary Production of the Biosphere: Integrating Terrestrial and Oceanic
Components, *Science*, 281, 237–240, <https://doi.org/10.1126/science.281.5374.237>, 1998.
- Gafar, N. A., Eyre, B. D., and Schulz, K. G.: Particulate inorganic to organic carbon production as a predictor for coccolithophorid sensitivity
to ongoing ocean acidification, *Limnology and Oceanography Letters*, 4, 62–70, <https://doi.org/10.1002/lol2.10105>, 2019.
- 390 Garcia, H. E., Weathers, K. W., Paver, C. C., Smolyar, I., Boyer, T. P., Locarnini, M. M., Zweng, M. M., Mishonov, A. V., Baranova, O. K.,
Seidov, D., and Reagan, J. R.: World Ocean Atlas 2018. Vol. 4: Dissolved Inorganic Nutrients (phosphate, nitrate and nitrate+nitrite,
silicate), Report, NOAA Atlas NESDIS 84, <https://archimer.ifremer.fr/doc/00651/76336/>, 2019a.
- Garcia, H. E., Weathers, K. W., Paver, C. R., Smolyar, I., Boyer, T. P., Locarnini, M. M., Zweng, M. M., Mishonov, A. V., Baranova, O. K.,
Seidov, D., and Reagan, J. R.: World Ocean Atlas 2018, Volume 3: Dissolved Oxygen, Apparent Oxygen Utilization, and Dissolved
395 Oxygen Saturation., Report, NOAA Atlas NESDIS 83, <https://archimer.ifremer.fr/doc/00651/76337/>, 2019b.
- Han, Y., Steiner, Z., Cao, Z., Fan, D., Chen, J., Yu, J., and Dai, M.: Coccolithophore abundance and production and their impacts on particulate
inorganic carbon cycling in the western North Pacific, *Biogeosciences*, 22, 3681–3697, <https://doi.org/10.5194/bg-22-3681-2025>, 2025.
- Hopkins, J. and Balch, W. M.: A New Approach to Estimating Coccolithophore Calcification Rates From Space, *Journal of Geophysical
Research: Biogeosciences*, 123, 1447–1459, <https://doi.org/10.1002/2017JG004235>, 2018.
- 400 Iglesias-Rodríguez, M. D., Brown, C. W., Doney, S. C., Kleypas, J., Kolber, D., Kolber, Z., Hayes, P. K., and Falkowski, P. G.: Representing
key phytoplankton functional groups in ocean carbon cycle models: Coccolithophorids, *Global Biogeochemical Cycles*, 16, 47–1–47–20,
<https://doi.org/10.1029/2001GB001454>, 2002.
- Kottmeier, D. M., Terbrüggen, A., Wolf-Gladrow, D. A., and Thoms, S.: Diel variations in cell division and biomass production of
Emiliana huxleyi—Consequences for the calculation of physiological cell parameters, *Limnology and Oceanography*, 65, 1781–1800,
405 <https://doi.org/10.1002/lno.11418>, 2020.



- Kottmeier, D. M., Chrachri, A., Langer, G., Helliwell, K. E., Wheeler, G. L., and Brownlee, C.: Reduced H^{+} channel activity disrupts pH homeostasis and calcification in coccolithophores at low ocean pH, *Proceedings of the National Academy of Sciences*, 119, e2118009 119, <https://doi.org/10.1073/pnas.2118009119>, 2022.
- Krumhardt, K. M., Lovenduski, N. S., Long, M. C., Levy, M., Lindsay, K., Moore, J. K., and Nissen, C.: Coccolithophore Growth and
410 Calcification in an Acidified Ocean: Insights From Community Earth System Model Simulations, *Journal of Advances in Modeling Earth Systems*, 11, 1418–1437, <https://doi.org/10.1029/2018MS001483>, 2019.
- Liu, H., Li, Q., Bai, Y., Yang, C., Wang, J., Zhou, Q., Hu, S., Shi, T., Liao, X., and Wu, G.: Improving satellite retrieval of oceanic particulate organic carbon concentrations using machine learning methods, *Remote Sensing of Environment*, 256, 112316, <https://doi.org/10.1016/j.rse.2021.112316>, 2021.
- 415 Locarnini, M. M., Mishonov, A. V., Baranova, O. K., Boyer, T. P., Zweng, M. M., Garcia, H. E., Reagan, J. R., Seidov, D., Weathers, K. W., Paver, C. R., and Smolyar, I.: *World Ocean Atlas 2018, Volume 1: Temperature*, Report, NOAA Atlas NESDIS 81, <https://archimer.ifremer.fr/doc/00651/76338/>, 2018.
- Maranón, E., Balch, W. M., Cermeno, P., González, N., Sobrino, C., Fernández, A., Huete-Ortega, M., López-Sandoval, D. C., Delgado, M., Estrada, M., et al.: Coccolithophore calcification is independent of carbonate chemistry in the tropical ocean, *Limnology and Oceanogra-*
420 *phy*, 61, 1345–1357, 2016.
- Marsh, N. L. J., Poulton, A. J., Mitchell, C., Balch, W. M., Marañón, E., Crawford, D. W., Álvarez, M., Blasco, D., Bowler, B. C., Cermeno, P., Drapeau, D. T., Feng, Y., Fernández-Carrera, A., Fernández, E., Fragoso, G. M., Gonzalez, N., Graziano, L. M., Holligan, Patrick, M., Hopkins, J., Huete-Ortega, M., Humphreys, M. P., Hutchins, D. A., Lam, P. J., Lipsen, M. S., Lopez-Sandoval, D., Loucaides, S., Marchetti, A., Mayers, K., Pelejero, C., Rees, A., Sobrino, C., Tynan, E., Tyrrell, T., Vidal, M., Whitney, F., and Daniels,
425 C. J.: Updated global compilation of coccolithophore calcification measurements from unperturbed water samples including ancillary data, <https://doi.org/10.1594/PANGAEA.987673>, 2025.
- Mitchell, C., Hu, C., Bowler, B., Drapeau, D., and Balch, W. M.: Estimating Particulate Inorganic Carbon Concentrations of the Global Ocean From Ocean Color Measurements Using a Reflectance Difference Approach, *Journal of Geophysical Research: Oceans*, 122, 8707–8720, <https://doi.org/10.1002/2017JC013146>, 2017.
- 430 Morel, A.: Optical modeling of the upper ocean in relation to its biogenous matter content (case I waters), *Journal of Geophysical Research: Oceans*, 93, 10 749–10 768, <https://doi.org/10.1029/JC093iC09p10749>, 1988.
- NASA Ocean Biology Processing Group: Aqua MODIS Level 3 Binned Chlorophyll Data, Version R2022.0, <https://doi.org/10.5067/AQUA/MODIS/L3B/CHL/2022>, 2022a.
- NASA Ocean Biology Processing Group: Aqua MODIS Level 3 Binned Remote-Sensing Reflectance Data, Version R2022.0,
435 <https://doi.org/10.5067/AQUA/MODIS/L3B/RRS/2022>, 2022b.
- Neukermans, G., Bach, L., Butterley, A., Sun, Q., Claustre, H., and Fournier, G.: Quantitative and mechanistic understanding of the open ocean carbonate pump - perspectives for remote sensing and autonomous in situ observation, *Earth-Science Reviews*, 239, 104359, <https://doi.org/10.1016/j.earscirev.2023.104359>, 2023.
- O'Reilly, J. E., Maritorena, S., Mitchell, B. G., Siegel, D. A., Carder, K. L., Garver, S. A., Kahru, M., and Mc-
440 Clain, C.: Ocean color chlorophyll algorithms for SeaWiFS, *Journal of Geophysical Research: Oceans*, 103, 24 937–24 953, <https://doi.org/10.1029/98JC02160>, 1998.
- Paasche, E.: A review of the coccolithophorid *Emiliania huxleyi* (Prymnesiophyceae), with particular reference to growth, coccolith formation, and calcification-photosynthesis interactions, *Phycologia*, 40, 503–529, 2001.



- Pedregosa, F., Varoquaux, G., Gramfort, A., Michel, V., Thirion, B., Grisel, O., Blondel, M., Prettenhofer, P., Weiss, R., Dubourg, V.,
445 Vanderplas, J., Passos, A., Cournapeau, D., Brucher, M., Perrot, M., and Duchesnay, E.: Scikit-learn: Machine Learning in Python, *Journal of Machine Learning Research*, 12, 2825–2830, 2011.
- Planchat, A., Kwiatkowski, L., Bopp, L., Torres, O., Christian, J. R., Butenschön, M., Lovato, T., Séférian, R., Chamberlain, M. A., Aumont, O., Watanabe, M., Yamamoto, A., Yool, A., Ilyina, T., Tsujino, H., Krumhardt, K. M., Schwinger, J., Tjiputra, J., Dunne, J. P., and Stock, C.: The representation of alkalinity and the carbonate pump from CMIP5 to CMIP6 Earth system models and implications for the carbon
450 cycle, *Biogeosciences*, 20, 1195–1257, <https://doi.org/10.5194/bg-20-1195-2023>, 2023.
- Poulton, A. J., Sanders, R., Holligan, P. M., Stinchcombe, M. C., Adey, T. R., Brown, L., and Chamberlain, K.: Phytoplankton mineralization in the tropical and subtropical Atlantic Ocean, *Global Biogeochemical Cycles*, 20, [https://doi.org/https://doi.org/10.1029/2006GB002712](https://doi.org/10.1029/2006GB002712), 2006.
- Poulton, A. J., Charalampopoulou, A., Young, J. R., Tarran, G. A., Lucas, M. I., and Quartly, G. D.: Coccolithophore dynamics in non-
455 bloom conditions during late summer in the central Iceland Basin (July–August 2007), *Limnology and Oceanography*, 55, 1601–1613, [https://doi.org/https://doi.org/10.4319/lo.2010.55.4.1601](https://doi.org/10.4319/lo.2010.55.4.1601), 2010.
- Poulton, A. J., Holligan, P. M., Charalampopoulou, A., and Adey, T. R.: Coccolithophore ecology in the tropical and subtropical Atlantic Ocean: New perspectives from the Atlantic meridional transect (AMT) programme, *Progress in Oceanography*, 158, 150–170, [https://doi.org/https://doi.org/10.1016/j.pocean.2017.01.003](https://doi.org/10.1016/j.pocean.2017.01.003), the Atlantic Meridional Transect programme (1995–2016), 2017.
- 460 Riebesell, U., Zondervan, I., Rost, B., Tortell, P. D., Zeebe, R. E., and Morel, F. M.: Reduced calcification of marine plankton in response to increased atmospheric CO₂, *Nature*, 407, 364–367, 2000.
- Robertson, J., Robinson, C., Turner, D., Holligan, P., Watson, A., Boyd, P., Fernandez, E., and Finch, M.: The impact of a coccolithophore bloom on oceanic carbon uptake in the northeast Atlantic during summer 1991, *Deep Sea Research Part I: Oceanographic Research Papers*, 41, 297–314, [https://doi.org/https://doi.org/10.1016/0967-0637\(94\)90005-1](https://doi.org/10.1016/0967-0637(94)90005-1), 1994.
- 465 Shutler, J. D., Land, P. E., Brown, C. W., Findlay, H. S., Donlon, C. J., Medland, M., Snooke, R., and Blackford, J. C.: Coccolithophore surface distributions in the North Atlantic and their modulation of the air-sea flux of CO₂ from 10 years of satellite Earth observation data, *Biogeosciences*, 10, 2699–2709, <https://doi.org/10.5194/bg-10-2699-2013>, 2013.
- Smith, S. V.: Parsing the Oceanic Calcium Carbonate Cycle: A Net Atmospheric Carbon Dioxide Source, or a Sink?, *Limnology and Oceanography e-Books*, Association for the Sciences of Limnology and Oceanography, Waco, Texas, ISBN 978-0-9845591-2-1,
470 <https://doi.org/10.4319/svsmith.2013.978-0-9845591-2-1>, 2013.
- Smith, S. V. and Gattuso, J.-P.: Balancing the Oceanic Calcium Carbonate Cycle: Consequences of Variable Water Column Ψ , *Aquatic Geochemistry*, 17, 327–337, <https://doi.org/10.1007/s10498-010-9109-9>, 2011.
- Tamsitt, V., Drake, H. F., Morrison, A. K., Talley, L. D., Dufour, C. O., Gray, A. R., Griffies, S. M., Mazloff, M. R., Sarmiento, J. L., Wang, J., and Weijer, W.: Spiraling pathways of global deep waters to the surface of the Southern Ocean, *Nature Communications*, 8, 172,
475 <https://doi.org/10.1038/s41467-017-00197-0>, 2017.
- Toullec, J.: Evaluation of the particulate inorganic carbon export efficiency in the global ocean, *Biogeosciences*, 23, 4361–4377, <https://doi.org/10.5194/bg-23-4361-2026>, 2026.
- Weber, T., Wiseman, N. A., and Kock, A.: Global ocean methane emissions dominated by shallow coastal waters, *Nature communications*, 10, 4584, 2019.



- 480 Zhuang, J., Dussin, R., Huard, D., Bourgault, P., Banihirwe, A., Raynaud, S., Malevich, B., Schupfner, M., Filipe, Levang, S., Gauthier, C.,
Jüling, A., Almansi, M., RichardScottOZ, RondeauG, Rasp, S., Smith, T. J., Stachelek, J., Plough, M., Pierre, Bell, R., Caneill, R., and Li,
X.: pangeo-data/xESMF: v0.8.2, <https://doi.org/10.5281/zenodo.8356796>, 2023.
- Ziveri, P., de Bernardi, B., Baumann, K.-H., Stoll, H. M., and Mortyn, P. G.: Sinking of coccolith carbonate and potential contribu-
tion to organic carbon ballasting in the deep ocean, *Deep Sea Research Part II: Topical Studies in Oceanography*, 54, 659–675,
485 <https://doi.org/https://doi.org/10.1016/j.dsr2.2007.01.006>, the Role of Marine Organic Carbon and Calcite Fluxes in Driving Global Cli-
mate Change, Past and Future, 2007.
- Ziveri, P., Gray, W. R., Anglada-Ortiz, G., Manno, C., Grelaud, M., Incarbona, A., Rae, J. W. B., Subhas, A. V., Pallacks, S., White, A., et al.:
Pelagic calcium carbonate production and shallow dissolution in the North Pacific Ocean, *Nature Communications*, 14, 805, 2023.
- Zondervan, I.: The effects of light, macronutrients, trace metals and CO₂ on the production of calcium carbonate and organic carbon in
490 coccolithophores—a review, *Deep Sea Research Part II: Topical Studies in Oceanography*, 54, 521–537, 2007.
- Zondervan, I., Zeebe, R. E., Rost, B., and Riebesell, U.: Decreasing marine biogenic calcification: A negative feedback on rising atmospheric
pCO₂, *Global Biogeochemical Cycles*, 15, 507–516, 2001.
- Zondervan, I., Rost, B., and Riebesell, U.: Effect of CO₂ concentration on the PIC/POC ratio in the coccolithophore *Emiliana huxleyi* grown
under light-limiting conditions and different daylengths, *Journal of Experimental Marine Biology and Ecology*, 272, 55–70, 2002.