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Reviews and syntheses: Experimental evidence of phytoplankton responses to Ocean Alkalinity Enhancement

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Abstract. Ocean alkalinity enhancement (OAE) has emerged as a promising carbon dioxide removal strategy aimed at increasing seawater alkalinity and enhancing long-term oceanic carbon uptake. However, concerns remain regarding the potential ecological impacts of large-scale alkalinity manipulation on marine planktonic communities, particularly phytoplankton, which play a central role in marine biogeochemical cycles and primary production. This review synthesizes the current experimental evidence on phytoplankton responses to different OAE approaches, including hydroxide-based, mineral-based, and bicarbonate-based treatments. We compare early conceptual predictions with recent laboratory, microcosm, mesocosm, and modelling studies, highlighting how the field has evolved from theoretical risk assessment toward increasingly mechanistic and experimentally grounded investigations. Current evidence generally indicates that phytoplankton communities exhibit a relatively high tolerance to moderate CO_2-equilibrated OAE scenarios, with limited effects on biomass, productivity, and community composition. More pronounced physiological and ecological responses are observed under unequilibrated or mineral dissolution treatments, where rapid pH shifts, trace metal release, and nutrient interactions may alter species-specific performance and community dynamics. Responses vary substantially across taxonomic groups and environmental contexts, reflecting the importance of carbonate chemistry, nutrient availability, and trace metal sensitivity in shaping OAE outcomes. Overall, existing studies suggest that phytoplankton responses to OAE are more nuanced and context-dependent than initially hypothesized, although substantial uncertainties remain regarding long-term ecosystem restructuring and large-scale biogeochemical feedback.

1 Study overview: introduction and methodological approach

Carbon dioxide removal (CDR) is increasingly recognized as a necessary component of climate mitigation strategies aimed at limiting global warming to 1.5–2 °C, as highlighted by recent IPCC assessments (2023, 2024). While deep reductions in greenhouse gas emissions remain essential, most mitigation scenarios incorporate CDR to offset residual emissions and manage temperature overshoot. Marine-based CDR (mCDR) approaches have gained prominence due to the ocean's central role in the global carbon cycle. Ocean alkalinity enhancement (OAE) has emerged as a promising mCDR strategy based on increasing seawater alkalinity to enhance atmospheric CO2 uptake and long-term carbon storage. However, the ecological

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implications of such alkalinity perturbations, particularly for marine phytoplankton communities that regulate primary production and biogeochemical feedback, remain only partially understood. This review synthesizes current knowledge on the interactions between OAE and phytoplankton, with emphasis on group-specific physiological and community-level responses.

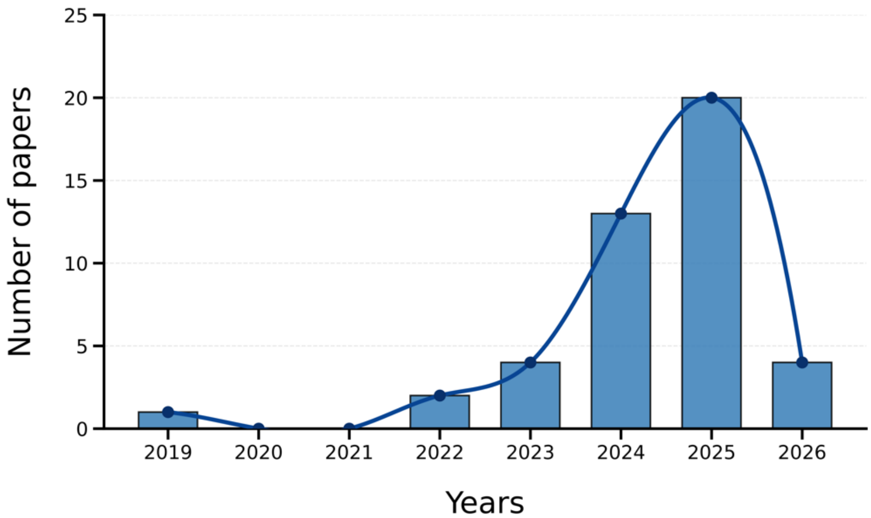

Figure 1: Temporal increase in the number of published studies investigating phytoplankton responses to OAE between 2019 and 2026. The curve illustrates the rapid recent growth of experimental and modelling research in the field.

The temporal evolution of the literature reveals a marked increase in research output over the past decade. This review is based on bibliometric data retrieved from the Scopus database. The search strategy was defined using the keywords “Ocean Alkalinity Enhancement” and “pH-equilibrated ocean alkalinization”, combined with biological descriptors including phytoplankton, plankton, diatoms, dinoflagellates, and coccolithophores, in order to capture relevant literature on marine microbial and algal responses. After a period of minimal activity between 2019 and 2021, the number of publications began to rise in 2022 and accelerated sharply through 2024 and 2025 (Figure 1). This trend likely reflects the increasing attention to CDR strategies within the broader context of climate mitigation, as well as growing recognition of the ocean’s potential role in long-term carbon storage. As of early 2026, the apparent decline in publication mirrors the incomplete nature of the current year’s record rather than a true decrease in research activity. On the contrary, continued growth in the number of studies is expected, although future research efforts may increasingly diversify toward higher trophic levels and ecosystem-scale responses, including zooplankton, fish, and broader food web dynamics, rather than focusing predominantly on phytoplankton alone. Overall, the rapid upward trajectory highlights OAE and its interactions with phytoplankton as emerging focal topics in marine biogeochemistry and climate intervention research.

The spatial distribution of studies further reveals a pronounced bias toward the Northern Hemisphere, with a concentration of research efforts in European regions, including the Northern Sea and the Mediterranean basin, as well as in parts of the North Atlantic (Figure 2). Additional studies are located along the eastern Atlantic margins, while comparatively few investigations have been conducted in the Southern Hemisphere, with only isolated efforts in regions such as Tasmania. This uneven distribution likely reflects disparities in research infrastructure, funding availability, and logistical accessibility.

In particular, the prominence of the North Sea as a study region can be attributed to a combination of scientific, logistical, and environmental factors that make it especially suitable for OAE research. The region hosts a dense network of marine

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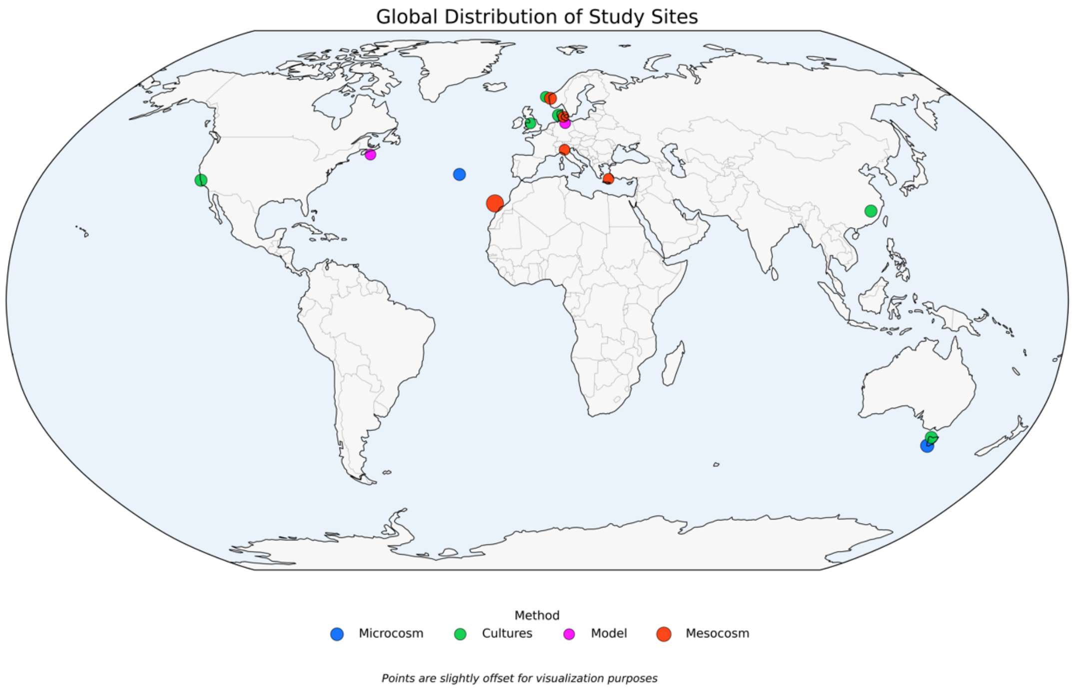

Figure 2: Global distribution of studies investigating phytoplankton responses to ocean alkalinity enhancement (OAE). Symbols indicate the main experimental approaches used in the reviewed literature, including modelling studies, laboratory cultures, microcosms, and mesocosms.

research institutions and long-term monitoring programs, enabling coordinated experimental efforts and high-frequency observations. Its relatively shallow depth and well-constrained circulation facilitate the detection and tracking of biogeochemical changes following alkalinity additions. Furthermore, the North Sea is characterized by dynamic yet well-studied plankton communities, strong seasonal bloom cycles, and relatively high nutrient availability, providing a responsive and measurable system in which ecological impacts can be readily observed. From a chemical perspective, the relatively high buffering capacity and elevated background alkalinity typical of many North Sea coastal waters, combined with strong air-sea exchange and mixing, may also enhance the detectability and short-term equilibration of carbonate system perturbations, making experimental manipulations both more controlled and more interpretable. These characteristics make it an ideal natural laboratory for testing OAE approaches under controlled conditions and in a more interpretable manner.

However, this bias toward the Northern Hemisphere also highlights a critical gap in current knowledge, as large and climatically relevant regions remain underrepresented. Expanding research across a broader range of oceanographic and biogeographical settings will be essential for developing a more comprehensive and globally representative understanding of phytoplankton responses to OAE.

In addition to their spatial distribution, existing OAE studies differ substantially in their methodological approaches (Figure 2), which strongly influence the interpretation and comparability of results. Current research spans a gradient of experimental complexity, including laboratory-based culture experiments, controlled microcosms, large-scale mesocosm

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studies, and modeling. Culture experiments provide high levels of control and mechanistic insight into species-specific physiological responses to altered carbonate chemistry, but they often lack ecological realism. Microcosm experiments incorporate simplified natural communities, allowing investigation of short-term interactions among taxa under controlled conditions, although they remain limited in scale and in environmental variability. Mesocosm studies represent an intermediate approach, capturing natural plankton communities and environmental dynamics while maintaining experimental control, and are therefore particularly valuable for assessing community-level responses and biogeochemical feedback.

In contrast, numerical models enable exploration of large-scale and long-term implications of OAE, including global biogeochemical cycling and ecosystem shifts, but rely heavily on parameterizations that are often constrained by limited empirical data. This diversity of approaches is essential for building a comprehensive understanding of OAE impacts, yet it also contributes to variability in reported outcomes. Differences in experimental design, duration, equilibration state, and alkalinity sources can lead to contrasting results across studies, highlighting the need for careful cross-scale integration when synthesizing current knowledge.

Phytoplankton comprise a diverse assemblage of unicellular, photoautotrophic microorganisms that convert dissolved inorganic carbon and nutrients into organic biomass and oxygen through photosynthesis. Global estimates indicate that marine phytoplankton account for approximately 50 Gt C yr^{-1} of primary production, a magnitude comparable to that of terrestrial vegetation (Field et al., 1998). As the dominant primary producers in the ocean, phytoplankton underpin marine ecosystem functioning and play a central role in regulating global carbon and nutrient cycles, while forming the base of marine food webs. The organic carbon they fix is transferred to higher trophic levels through zooplankton and fish, and the release of dissolved and particulate organic matter fuels large and diverse heterotrophic bacterial communities. Phytoplankton also engage in diverse microbial interactions that influence nutrient cycling and ecosystem functioning. Within the phycosphere, close associations with heterotrophic bacteria facilitate the exchange of metabolites and nutrients, with bacteria benefiting from phytoplankton-derived dissolved organic matter and, in some cases, supplying essential compounds such as vitamins (Amin et al., 2012; Seymour et al., 2017). Through these pathways, phytoplankton sustain ecosystem productivity, biodiversity, and a wide range of ecosystem services. Beyond their ecological role, phytoplankton exert a strong influence on air–sea CO_2 exchange and long-term carbon sequestration in the ocean interior. Their activity drives the biological carbon pump (BCP), whereby photosynthetically fixed carbon is transformed into particulate and dissolved organic carbon (POC and DOC) and exported below the euphotic zone. Export occurs via gravitational sinking of marine snow, active transport associated with zooplankton vertical migration, and physical processes such as subduction and overturning circulation. In parallel, the carbonate pump involves the formation of biogenic calcium carbonate by marine calcifiers, providing ballast that enhances the sinking of both inorganic carbon and associated organic matter. Environmental conditions, including nutrient limitation (e.g., silica depletion in diatoms), can alter phytoplankton physiology by impairing buoyancy regulation and promoting the release of carbon-rich extracellular material, thereby enhancing aggregate formation and vertical export. Through these interconnected processes, phytoplankton not only regulate marine productivity but also

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influence global biogeochemical cycles and climate by modulating atmospheric concentrations of CO_2 and other greenhouse gases, such as nitrous oxide (N_2O).

This review aims to synthesize the current experimental evidence on phytoplankton responses to ocean alkalinity enhancement (OAE), integrating findings from laboratory cultures, microcosm and mesocosm experiments, and modeling studies. Particular attention is given to how different OAE approaches influence phytoplankton physiology, community composition, and ecosystem functioning, with the goal of identifying emerging patterns, key uncertainties, and future research directions.

2 Types of Ocean Alkalinity Enhancement

OAE approaches can be broadly classified according to the dominant chemical form of alkalinity addition and the associated mechanism through which alkalinity is released into seawater. These differences determine the magnitude of pH perturbation, the release of nutrients and trace metals, and the resulting ecological responses of marine phytoplankton communities.

2.1 Hydroxide-based alkalinity enhancement

Hydroxide-based OAE involves the direct addition of alkaline compounds such as sodium hydroxide (NaOH), calcium hydroxide ($Ca(OH)_2$), or magnesium hydroxide ($Mg(OH)_2$). These approaches create rapid, localized pH changes that must be distinguished between equilibrated and unequilibrated scenarios. In equilibrated treatments where CO_2 and pH are small, hydroxide-based OAE had minimal effects on coastal plankton communities (Kousoulas et al., 2025). However, in unequilibrated treatments simulating the immediate post-dispersal conditions, there were slight delays in phytoplankton blooms and reorganization of diatom communities (Kousoulas et al., 2025). A liming experiment in the eastern Mediterranean showed that while chlorophyll-a and heterotrophic bacteria remained stable, S*ynechococcus* and dinoflagellates increased, while diatoms and ciliates declined (Traboni et al., 2025).

A novel approach to hydroxide-based OAE is named pH-equilibrated Ocean Alkalinization, which fundamentally differs from traditional hydroxide-based approaches by premixing and pre-equilibrating the alkaline solution before ocean discharge (Jamali Alamooti et al., 2026). Instead of adding reactive calcium hydroxide or sodium hydroxide directly to seawater, which causes abrupt local pH spikes and turbidity, the Limenet® process involves the controlled production of calcium bicarbonate in a terrestrial reactor where limestone (calcium carbonate) is calcined, converted to calcium hydroxide, and then reacted with captured CO_2 in seawater within the reactor vessel. This produces a transparent aqueous solution of calcium bicarbonate with the same pH as natural seawater, which is then discharged into the ocean in a pre-equilibrated state.

Recent developments in OAE include brucite-inspired alkalinity addition (BIAA), which uses $MgCl_2$ x $6H_2O$ and NaOH to achieve increased alkalinity (Welch et al., 2025). The term “brucite-inspired” refers to the fact that this approach mimics the

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chemistry of the mineral brucite, which naturally releases hydroxide ions in water, increasing alkalinity and promoting CO_2 conversion to bicarbonate (Welch et al., 2025). Laboratory experiments with natural Santa Barbara Channel phytoplankton communities revealed differential impacts on phytoplankton functional groups, with reduced contributions of diatoms and enhanced abundances of Prymnesiophyceae (coccolithophores and *Phaeocystis* sp.) (Welch et al., 2025). This approach demonstrates that specific chemistry of the alkalinity source can drive species-specific responses independent of alkalinity increase alone.

2.2 Carbonate-based alkalinity enhancement

Carbonate-based OAE involves the addition of carbonate salts such as sodium bicarbonate ($NaHCO_3$) and sodium carbonate (Na_2CO_3) to seawater. This approach represents one of the most chemically controlled forms of OAE, as it directly increases total alkalinity (TA) without releasing additional bioactive chemicals (Ramirez et al., 2025). A mesocosm study conducted in subtropical Atlantic waters tested a gradient of TA from 2400 to 4800 $\mu molL^{-1}$, demonstrating that carbonate-based OAE with CO_2 equilibration does not cause widespread cellular stress in phytoplankton communities during the immediate post-treatment period (Ramirez et al., 2025). The carbonate approach offers predictability in terms of carbonate chemistry changes, making it useful for controlled experimental assessments of OAE impacts (González-Santana et al., 2024).

2.3 Silicate-based alkalinity enhancement

Mineral-based OAE employs pulverized silicate minerals to increase seawater alkalinity. The most commonly tested mineral is olivine (primarily Mg_2SiO_4), which releases silicate nutrients, trace metals (including Ni and Fe), and alkalinity during dissolution (Guo et al., 2024). Olivine-based OAE has been associated with positive responses in diatoms, likely linked to silicate release and nutrient alleviation effects. In experiments from the Equatorial Pacific, sodium hydroxide had negligible effects on phytoplankton while providing predictable alkalinity, whereas olivine disrupted plankton communities, particularly affecting cyanobacteria, heterotrophic bacteria, and picoeukaryotes (Guo et al., 2025).

3 Effects of OAE on phytoplankton communities and community shifts

3.1 Community responses

Research examining CO_2-equilibrated OAE in oligotrophic systems demonstrates that phytoplankton and microzooplankton show

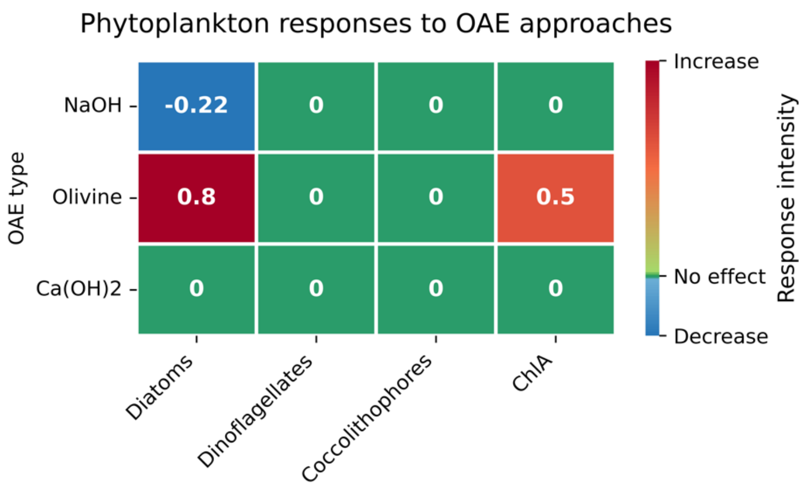

Figure 3: Semi-quantitative heatmap summarizing phytoplankton responses to different ocean alkalinity enhancement (OAE) approaches. Response scores were assigned to each study as negative (−1), neutral (0), or positive (+1), and averaged across studies for each phytoplankton group and OAE methodology. Blue colours indicate negative responses, green indicates neutral effects, and red indicates positive responses.

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remarkably high tolerance to increases in alkalinity. In a mesocosm study in the subtropical North Atlantic, the abundance and biomass of phytoplankton and microzooplankton were insensitive to OAE across all size classes (pico, nano and micro), nutritional modes (autrophic, mixotrophic and heterotrophic), and taxonomic groups examined, including cyanobacteria, diatoms, haptophytes, dinoflagellates and ciliates (Xin et al., 2024). Consequently, plankton communities maintained their natural chlorophyll-a levels, size structure, taxonomic composition, and biodiversity under CO_2-equilibrated OAE (Xin et al., 2024). However, the type and implementation approach of OAE substantially influence community responses. A coastal Tasmania study found that simulated OAE had significant but generally moderate effects on various phytoplankton and heterotrophic bacteria groups, with more pronounced effects on diatom silicic acid drawdown and biogenic silica build-up reduced at elevated alkalinity (Ferderer et al., 2022). To synthesize the growing body of experimental evidence, a heatmap was constructed to compare the direction and magnitude of phytoplankton responses across major functional groups under different OAE approaches (Figure 3). A semi-quantitative response scoring approach was applied, in which individual studies were assigned negative (−1), neutral (0), or positive (+1) scores based on the predominant direction of the reported biological response and averaged across studies for each phytoplankton group and OAE methodology. The heatmap highlights clear differences in phytoplankton responses depending on the type of OAE applied. Olivine is associated with strongly positive responses in diatoms and increases in chlorophyll-a, likely reflecting the release of dissolved silicate and micronutrients that alleviate nutrient limitation. In contrast, hydroxide-based approaches such as NaOH show neutral to slightly negative responses, consistent with their primary effect on carbonate chemistry without additional nutrient inputs. Notably, responses for dinoflagellates and coccolithophores appear largely neutral or underrepresented, reflecting either a true lack of sensitivity or, more likely, the limited number of studies addressing these groups. Overall, the synthesis suggests that OAE impacts are highly dependent on the chemical nature of the alkalinity source, with nutrient-mediated effects playing a key role in shaping community responses. Although this approach does not represent a formal meta-analysis, it provides a comparative overview of general response patterns emerging across the current literature.

3.2 Diatoms

Diatoms generally exhibit a high degree of resilience to moderate ocean alkalinity enhancement, with growth rates and elemental stoichiometry remaining largely unchanged under limestone- or calcium-based alkalinization (Gately et al., 2023). However, diatom responses are strongly genus- and species-specific and depend on the mineralogical composition of the alkalinity source rather than on alkalinity increases alone. Mesocosm experiments demonstrate that silicate-based OAE significantly enhances diatom silicification through increased dissolved silicate availability, whereas calcium-based OAE has limited effects, influencing silicification in only a subset of genera such as *Pseudo-nitzschia* and *Nitzschia* (Ferderer et al., 2024). In contrast, other genera including *Arcocellulus*, *Cylindrotheca*, *Skeletonema*, and *Thalassiosira* show no significant silicification response across alkalinity increases of up to 600 µmol kg^{-1}, indicating that genus-specific impacts are primarily driven by nutrient supply rather than alkalinity *per se* (Ferderer et al., 2024). Recent field-based evidence further supports the overall tolerance of diatom communities to OAE. In a coastal alkalinity enhancement experiment, Groppelli et al. (2026) reported no significant changes in diatom biomass or community composition under moderate alkalinity additions, despite

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measurable shifts in carbonate chemistry. However, subtle physiological responses were observed, including changes in silica cycling, suggesting that diatom-mediated biogeochemical processes may respond to OAE even in the absence of pronounced community-level shifts. Additional species-specific sensitivities may arise from trace metal release associated with certain OAE materials; for example, *Thalassiosira weissflogii* exhibits strong growth inhibition at elevated nickel concentrations resulting from olivine dissolution (Xin et al., 2024). In natural coastal communities, OAE has also been associated with reduced silicic acid drawdown and increased biogenic silica accumulation, indicating moderate but ecologically relevant alterations of diatom biogeochemistry (Ferderer et al., 2022). Overall, these findings indicate that diatoms are broadly tolerant to OAE, but their physiological and biogeochemical responses are modulated by mineral-specific nutrient and trace metal inputs.

3.3 Dinoflagellates

Dinoflagellates generally exhibit more variables and, in several cases, higher sensitivity to ocean alkalinity enhancement compared to diatoms. Available evidence suggests that dinoflagellate growth responses to OAE-induced changes in carbonate chemistry are primarily driven by variations in pH and CO_2 rather than bicarbonate availability, resulting in significant differences in fitness relative to other phytoplankton groups (Oberlander et al., 2025). Microcosm experiments indicate that dinoflagellate abundance often shows moderate responses under low OAE dosages but declines at higher alkalinity levels, with response patterns comparable to those observed for coccolithophores and, in some cases, diatoms (Bazzicalupo et al., 2024). Dinoflagellate sensitivity to OAE appears to be amplified under extreme alkalinity conditions or when alkalinity enhancement is associated with the release of trace metals, although the limited number of studies precludes definitive conclusions. Species-specific responses further highlight this variability. For example, the invasive dinoflagellate *Noctiluca scintillans* exhibits contrasting responses depending on the OAE approach and equilibration state: its abundance decreased under unequilibrated hydroxide-based (NaOH) treatments but showed little to no response under pH-equilibrated alkalinity additions, while olivine-based treatments applied to Tasmanian plankton communities resulted in marked reductions in abundance (Guo et al., 2024; Kousoulas et al., 2025). These findings suggest that dinoflagellate responses may be driven more by rapid perturbations in pH and pCO_2 than by equilibrated increases in alkalinity, with potential implications for community composition and invasive species dynamics under localized OAE deployment.

3.4 Coccolithophores

Coccolithophores, which are major contributors to phytoplankton communities and global ocean biogeochemistry (Balch, 2018), represent a functionally distinct calcifying group with unique sensitivities to OAE. The most widespread species, *Emiliania huxleyi*, exhibits threshold-based growth responses to alkalinity enhancement. In controlled culture experiments, *E. huxleyi* growth rates diminished above a total alkalinity increase of approximately 600 μmol kg^{-1}, suggesting a threshold CO_2 concentration of around 100 μatm necessary for optimal growth (Faucher et al., 2025). This threshold response contrasts with many non-calcifying phytoplankton groups that show more gradual responses to carbonate chemistry changes. The cellular calcite-to-organic carbon ratio (PIC:POC) of *E. huxleyi* remained stable across a wide total alkalinity range, suggesting that while growth rates respond to elevated alkalinity, the stoichiometry of calcification relative to photosynthesis

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does not change dramatically (Faucher et al., 2025). In mesocosm experiments simulating calcium- and silicate-based mineral OAE in a temperate fjord ecosystem, coccolithophore calcification followed an optimum curve response along the pCO_2 gradient, with a maximum calcification occurring at intermediate pCO_2 values (Schneider et al., 2026). This response pattern is consistent with findings from monospecific laboratory cultures, suggesting that field conditions do not fundamentally alter the physiological constraints on calcification. Notably, zooplankton respiration was negatively correlated with pCO_2, suggesting indirect ecosystem effects mediated by grazing pressure on coccolithophores (Schneider et al., 2026). Field-based coccolithophore mesocosm experiments revealed mixed responses depending on experimental conditions. In nutrient-limited conditions, coccolithophore abundances remained largely unaffected across different OAE treatments during the oligotrophic phase of an experiment but showed significant negative responses to increasing alkalinity treatment during nutrient-enriched conditions (Xin et al., 2024). A slightly positive correlation to slurry concentrations was observed, whereas high concentrations were detrimental to coccolithophore abundance (Bazzicalupo et al., 2024). These findings suggest that coccolithophore responses are context-dependent, mediated by both carbonate chemistry and nutrient availability. Laboratory experiments with limestone-inspired alkalinity additions (moderate ~700 and high ~2700 µmol kg^{-1}) demonstrated that *E.huxleyi* exhibited neutral growth responses to alkalinity perturbations in terms of both growth rates and elemental ratios (Gately et al., 2023). However, abiotic mineral precipitation occurred during these experiments, removing nutrients and alkalinity from solution, which complicates the interpretation of the net ecological impacts (Gately et al., 2023). Coccolithophores show differential sensitivity to trace metal perturbations associated with mineral-based OAE. The coccolithophore *E.huxleyi* exhibited a relatively mild growth rate inhibition (approximately 30%) at the highest nickel concentrations (100 µmol L^{-1}) tested, with an IC50 exceeding the tested range (Xin et al., 2024). This suggests coccolithophores are more tolerant to elevated nickel than diatoms but potentially less so than some other phytoplankton groups, supporting the hypothesis that specific metal sensitivities create opportunities for community restructuring under mineral-based OAE.

3.5 Community succession and bloom timing

OAE implementation approaches that cause more severe carbonate chemistry perturbations can alter the timing of phytoplankton blooms and community succession patterns. In unequilibrated OAE treatments in Norwegian fjord waters, mild delays in bloom formation were observed, related, though not directly proportional, to the TA gradient (Marín-Samper et al., 2024). These delays were more pronounced for calcium-based treatments compared to silicate-based treatments, with low TA treatments exhibiting earlier responses than high TA ones. The delay was likely due to species-specific negative relationships between high-pH/low-pCO_2 conditions and phytoplankton growth rates (Marín-Samper et al., 2024). In a Tasmanian fjord study examining diatom-dominated spring blooms, unequilibrated OAE caused a slight reorganization of the diatom community before the bloom reached its maximum chlorophyll-a level, though the overall community remained diatom-dominated (Kousoulas et al., 2025). These findings suggest that while gross community structure may be preserved, fine-scale compositional changes within dominant functional groups can occur, particularly when carbonate chemistry perturbations are most extreme.

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3.6 Responses and cellular health

Multiple studies report minimal evidence of cellular stress on physiological impairment in phytoplankton communities exposed to OAE. In a 33-day mesocosm experiment with natural subtropical Atlantic plankton, photosynthetic efficiency (Fv/Fm) initially declined during phase I (days 5-20), but this change was not accompanied by significant increases in reactive oxygen species (ROS) levels (Ramírez et al., 2025). During phase II (days 21-33), pronounced community responses included the emergence of blooms of large-size nanoeukaryotes from *Chrysochromulina*, increases in chlorophyll-a and accessory pigments, and flourishing *Synechococcus* spp. (Ramírez et al., 2025). The pigment ratios DD+DT:FUCO and DD+DT:Chl-a increased in medium TA treatments, indicating enhanced investment in photoprotective pigments. This response may reflect shifts in cellular energy allocation under altered carbonate chemistry, potentially linked to changes in nutrient utilization rather than acute physiological stress (Ramírez et al., 2025). Together, these results suggest that OAE does not induce acute cellular stress but rather triggers a physiological reorganization. The transient decrease in photosynthetic efficiency, in the absence of increased ROS production, indicates acclimation rather than damage. Concurrent increases in photoprotective pigment ratios further support a shift in energy allocation, while the emergence of blooms and increased biomass demonstrate that phytoplankton communities remain functionally active and capable of reorganizing under altered carbonate chemistry conditions.

4 Mechanisms: carbonate chemistry, trace metals, and nutrient effects

4.1 Carbonate chemistry alterations

The primary mechanism through which OAE affects phytoplankton communities is through changes in seawater carbonate speciation. Enhanced alkalinity increases bicarbonate ion concentrations and carbonate saturation states, thereby reducing the partial pressure of CO2 (pCO_2) and increasing pH before atmospheric re-equilibration (Schneider et al., 2026). These chemical changes have differential effects depending on the implementation approach. CO_2-equilibrated OAE maintains moderate carbonate chemistry perturbation compared to unequilibrated approaches, resulting in relatively benign ecosystem effects in oligotrophic systems (Suessle et al., 2025).

However, mineral precipitation presents a critical challenge to OAE efficiency. Shipboard microcosm experiments in the North Atlantic demonstrated that mineral precipitation takes place over timescales of hours to days, with aragonite as the dominant precipitate phase (Hashim et al., 2025). The precipitation rate correlates with aragonite saturation state, and precipitation can occur in a runaway manner, decreasing total alkalinity to values below those of seawater prior to alkalinity addition (Hashim et al., 2025). This has direct implications for phytoplankton communities, as it removes nutrients and alkalinity from solution simultaneously (Gately et al., 2023).

4.2 Trace metals effects

The release of trace metals during mineral-based OAE dissolution presents species-specific phytoplankton responses. Nickel (Ni), one of the most abundant metals in OAE source materials such as olivine, showed variable impacts on phytoplankton. The coccolithophore *Emiliania huxleyi* and the dinoflagellate *Amphidinium carterae* exhibited growth rate inhibition of about 30% and 20%, respectively, at the highest Ni concentrations (100µmol L^{-1}) (Xin et al., 2024). In contrast, the diatom

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Thalassiosira weissflogii displayed considerably higher sensitivity to Ni, with 60% growth rate inhibition at the highest Ni concentration (Xin et al., 2024). This demonstrates important differential sensitivities between taxonomic groups that could alter community composition under OAE with Ni-rich mineral sources.

Olivine dissolution products, which include Fe, Si, and trace metals, produced both positive and neutral responses but no evident toxic effects on six representative phytoplankton species tested (Hutchins et al., 2023). Both single and competitive co-cultures showed that silicifying diatoms and calcifying coccolithophores benefited from olivine dissolution products through enhanced iron and silicate availability, or enhanced alkalinity, respectively (Hutchins et al., 2023). Iron complexation patterns appear resistant to OAE-induced changes; in a mesocosm study where carbonate salts were added, over 99% of iron remained complexed, and phytoplankton remained unaffected by alterations in iron dynamics (González-Santana et al., 2024).

4.3 Nutrient dynamics and bioavailability

Ocean alkalinity enhancement influences marine plankton not only through direct modifications of carbonate chemistry but also via indirect effects mediated by nutrient availability and trophic interactions. In the North Atlantic, OAE was shown to consistently reduce phytoplankton abundance under both natural and nutrient-enriched conditions, potentially as a result of CO_2 limitation leading to decreased production of phytoplankton-derived organic matter (de Castro et al., 2025). This decline was accompanied by reduced leucine aminopeptidase activity and shifts in the composition of phytoplankton-associated bacterial communities, indicating cascading effects on microbial food webs. In contrast, responses in nutrient-limited systems appear to be non-linear along alkalinity gradients. In oligotrophic mesocosm experiments, net community production (NCP), gross production (GP), and community respiration (CR) exhibited curvilinear responses to increasing total alkalinity, with maxima in NCP and transitions from heterotrophic to autotrophic metabolic states at intermediate alkalinity levels (approximately 1500–1800 μmol L^{-1}) (Marín-Samper et al., 2024). These metabolic peaks coincided with increases in nanoplankton abundance, size fractionated chlorophyll-a, and ^{14}C uptake, suggesting that OAE may transiently alleviate nutrient limitation under specific chemical conditions. However, in nutrient-rich mesocosms, increasing alkalinity combined with nutrient additions elicited negative responses in coccolithophores, highlighting that OAE nutrient interactions are strongly context dependent and can shift from stimulatory to inhibitory depending on trophic status and the magnitude of alkalinity addition (Xin et al., 2024).

5 Current knowledge and future research needs

5.1 What we know

Early conceptual work on ocean alkalinity enhancement, such as the study by Bach et al. (2019), primarily focused on large-scale biogeochemical implications and potential risks associated with mineral dissolution products, rather than on direct experimental observations of phytoplankton responses. In that framework, OAE was hypothesized to substantially alter marine pelagic ecosystems through changes in carbonate chemistry and the release of nutrients and trace metals, potentially favoring specific functional groups such as calcifiers and silicifiers and giving rise to contrasting scenarios such as a “green ocean”, characterized by enhanced primary production, or a “white ocean”, dominated by increased calcification. In contrast,

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the more recent body of literature synthesized in this review reflects a shift toward experimentally grounded, process-oriented studies, including laboratory cultures and mesocosm experiments. These studies generally indicate that phytoplankton communities exhibit a high tolerance to moderate CO_2-equilibrated OAE, with limited impacts on biomass, diversity, and overall productivity, while more pronounced effects emerge under unequilibrated or mineral-based treatments that introduce additional chemical stressors. Importantly, while early hypotheses suggested potentially large-scale shifts toward specific functional groups driven by nutrient enrichment and carbonate chemistry changes, empirical evidence to date points to more nuanced, context-dependent responses, often mediated by species-specific physiology, nutrient availability, and trace metal sensitivity. This highlights a key evolution in the field from theoretical risk assessment toward a more mechanistic and experimentally validated understanding of OAE phytoplankton interactions, while also underscoring persistent uncertainties regarding long-term ecosystem restructuring and biogeochemical feedback.

Emerging consensus from mesocosm and laboratory studies indicates that CO_2-equilibrated OAE, implemented at moderate alkalinity levels in oligotrophic systems, produces minimal direct toxic effects on phytoplankton communities. Phytoplankton show high tolerance to carbonate chemistry perturbations in the short term (days or weeks), with most communities maintaining their natural taxonomic composition and size structure. Different OAE implementation approaches produce vastly different ecological impacts: mineral-based approaches release bioactive substances with species-specific effects, whereas chemical alkalinity sources (carbonates, hydroxides) primarily alter carbonate chemistry with secondary nutrient effects. Community-level responses appear modulated by nutrient availability, pre-existing community composition, and local environmental conditions. Oligotrophic systems show greater resilience to OAE perturbations than potentially nutrient-limited systems. Specific phytoplankton groups, particularly diatoms, dinoflagellates, and coccolithophores, show species-specific responses.

5.2 Critical knowledge gaps

Despite advances, significant uncertainties remain regarding OAE's long-term ecological impacts. First, the vast majority of OAE research has employed CO_2 equilibrated approaches that likely underestimate environmental perturbations compared to field-deployed scenarios where water is not pre-equilibrated with atmospheric CO_2. Most real-world deployment scenarios will involve unequilibrated alkalinity additions with more severe pH/pCO_2 changes (Schneider et al., 2026), yet ecosystem responses to such conditions remain poorly characterized.

Second, interactions between OAE and ongoing climate change (warming, acidification, deoxygenation) remain unexamined. Most studies employ current-day temperature and nutrient regimes; how phytoplankton will respond to combined OAE, and climate stressors remains speculative.

5.3 Recommended research priorities

To advance Ocean Alkalinity Enhancement (OAE) as an evidence-based marine carbon dioxide removal (CDR) strategy, future research should prioritize ecosystem-level studies that examine impacts across multiple trophic levels and seasonal cycles (Goldenberg et al., 2024), alongside evaluations of non-equilibrated OAE approaches that better reflect realistic field conditions (Schneider et al., 2026). Particular attention should also be given to the assessment of OAE performance across

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diverse marine environments, including systems characterized by contrasting nutrient regimes, temperature ranges, and biodiversity structures, as well as to the definition of safe operating spaces that identify alkalinity thresholds and mineral amendments that minimize ecological risks (Bednarek et al., 2025). In parallel, there is a need to investigate potential synergistic effects among different OAE implementation strategies, species-specific responses within key functional groups, and the possibility of genetic adaptation under sustained alkalinity perturbations, which will be critical for understanding long-term ecosystem trajectories under large-scale deployment scenarios. Finally, the development of standardized experimental and monitoring protocols would greatly enhance comparability and synthesis across studies, while still accounting for the inherent variability among marine ecosystems and ocean basins.

6 Conclusions

Ocean alkalinity enhancement represents a technologically feasible approach to large-scale atmospheric CO_2 removal, but its ecological implications for marine phytoplankton is only partially understood. Current evidence suggests that moderate CO_2-equilibrated OAE produces minimal acute disruption to phytoplankton communities in oligotrophic systems, with high tolerance across size classes and nutritional modes. However, the choice of alkalinity source critically determines ecological impacts. Phytoplankton exhibit distinct, species-specific responses that cannot be generalized by functional groups, with implications for biogeochemical cycling and food web dynamics. Moving forward, translating OAE from controlled laboratory and mesocosm studies to large scale ocean deployment will require more research on ecosystem responses under realistic deployment conditions, across diverse biogeographic areas and over timescales extending beyond current experimental durations.

Author contributions

SG: Conceptualization, Data curation, Formal analysis, Investigation, Visualization, Writing (original draft preparation), Writing (review and editing). DB: Conceptualization, Supervision, Writing (review and editing).

Competing interests

The authors declare that they have no conflict of interest.

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