

Earth's Future

REVIEW ARTICLE

10.1029/2026EF009044

Key Points:

- Moderate alkalinity may cut pH-control costs, freeing energy for thicker, denser tests in larger benthic foraminifera
- Hierarchical geochemical and morphological proxies track OAE alkalinity effects in benthic foraminifera
- XRD/SEM/Raman reveal stress and ultrastructure shifts, assessing calcification quality beyond size

Correspondence to:

G. Henry,
g.rizkallah@campus.unimib.it;
gmina@sci.cu.edu.eg

Citation:

Henry, G., & Basso, D. (2026). Calcareous benthic foraminifera under Ocean Alkalinity Enhancement: Synthesis, knowledge gaps, and future research agenda. *Earth's Future*, 14, e2026EF009044. <https://doi.org/10.1029/2026EF009044>

Received 6 JUN 2026

Accepted 11 AUG 2026

Author Contributions:

Conceptualization: George Henry, Daniela Basso
Data curation: Daniela Basso
Formal analysis: George Henry
Funding acquisition: Daniela Basso
Methodology: George Henry
Project administration: Daniela Basso
Supervision: Daniela Basso
Validation: George Henry
Writing – original draft: George Henry
Writing – review & editing: Daniela Basso

Calcareous Benthic Foraminifera Under Ocean Alkalinity Enhancement: Synthesis, Knowledge Gaps, and Future Research Agenda

George Henry^{1,2}  and Daniela Basso¹ 

¹Department of Earth and Environmental Sciences (DISAT), University of Milano-Bicocca, Milano, Italy, ²Geology Department, Faculty of Science, Cairo University, Giza, Egypt

Abstract Limiting global warming to 1.5°C will require carbon dioxide removal, and Ocean Alkalinity Enhancement (OAE) is increasingly being explored as a marine carbon dioxide removal pathway. However, benthic biological responses remain much less constrained than water-column processes and planktonic responses, even though calcareous benthic foraminifera play important roles in sediment–water interface biogeochemistry and coastal carbonate budgets. This review synthesizes current understanding of benthic foraminiferal biomineralization, experimental evidence relevant to elevated alkalinity, and analytical approaches for detecting OAE-driven changes in test structure and chemistry. Available evidence indicates that calcification in benthic foraminifera is a tightly regulated, energy-dependent process controlled by the interaction between inorganic-carbon supply, biological pH regulation, and external carbonate chemistry. While inverse analogs such as ocean acidification studies provide mechanistic clues regarding species-specific sensitivities, direct experimental evidence of benthic foraminiferal responses to true OAE conditions remains a critical knowledge gap. We propose an analytical framework that integrates morphometric measurements, X-ray diffraction, Raman spectroscopy, SEM/micro-CT imaging, and calibrated geochemical proxies such as $\delta^{11}\text{B}$, U/Ca, and selected element ratios to distinguish primary biomineralization responses from redox, nutrient, and diagenetic overprints. We propose a four-tier framework for geochemical proxies that links primary carbonate-system indicators with feedstock-related tracers and quality-control metrics for interpreting OAE-driven perturbations. The framework proposed here enables cross-calibrated workflows for laboratory, mesocosm, and field settings, supporting evaluation of benthic responses, refining environmental assessment, and identifying where foraminiferal observations may inform OAE efficacy and benthic feedbacks on alkalinity retention.

Plain Language Summary To combat global warming, Ocean Alkalinity Enhancement (OAE)—which involves adding substances like lime or olivine to the ocean to absorb more carbon dioxide—has shown promise. However, the impact of OAE on marine life, especially on the seafloor, remains underexplored. Our study focuses on benthic foraminifera as valuable indicators for monitoring the effects of OAE. We show that the process of building these shells is energy-intensive and highly regulated. Our findings suggest that moderate increases in ocean alkalinity might reduce the energy costs for these organisms, allowing them to produce thicker, more resilient shells, particularly in larger foraminifera. We propose a three-stage framework for assessing foraminiferal responses. The first stage measures shell growth and dimensions, the second quantifies changes in shell carbonate mass, and the third uses imaging and mineralogical techniques—including SEM, micro-CT, XRD, and Raman spectroscopy. We also organize geochemical indicators into four functional groups: carbonate-system proxies, feedstock-related tracers, biomineralization-sensitive indicators, and quality-control measures. This research is crucial for developing standardized testing methods to predict the long-term ecological effects of OAE. By incorporating data from foraminifera into OAE monitoring, we can improve our ability to assess and ensure the success of these climate-mitigation strategies.

1. Introduction

The Intergovernmental Panel on Climate Change (IPCC) has emphasized that limiting global warming to 1.5°C above pre-industrial levels will require not only emissions reductions but also carbon dioxide removal (CDR) approaches (Dale et al., 2024; IPCC, 2021). Among marine CDR options, Ocean Alkalinity Enhancement (OAE) has received growing attention. Increasing seawater alkalinity enhances the ocean's capacity to absorb

atmospheric CO₂ and helps counteract ocean acidification. OAE is also considered potentially scalable and technically viable because alkaline feedstocks are widely available and several proposed pathways rely partly on established mineral-processing, chemical-engineering, and electrochemical technologies (Eisaman et al., 2023; Oschlies et al., 2023; Renforth & Henderson, 2017). Importantly, OAE is not a single intervention. Alkalinity can be delivered as reactive solids, such as lime (CaO), hydrated lime (Ca(OH)₂), brucite, or silicate minerals. It can also be added as aqueous solutions such as NaOH_(aq) through coastal enhanced weathering using minerals like basalt or peridotite, or by electrochemical removal of acid from seawater (Eisaman et al., 2023; Fennel et al., 2023). These pathways differ in feedstock, dispersal mode, equilibration state, and environmental setting. As a result, their near-field chemistry and ecological consequences also differ. Such differences are biologically important. The magnitude and duration of carbonate-chemistry perturbation, and the extent of benthic habitat exposure, depend on where and how alkalinity is introduced—specifically, whether the intervention remains confined to the surface water column or directly settles onto the seafloor (Cyronak et al., 2023; Eisaman et al., 2023). A major technical constraint is secondary CaCO₃ precipitation, which consumes added alkalinity and can reduce net CO₂ removal efficiency (Moras et al., 2022; Renforth & Henderson, 2017). Experimental work shows that this risk is strongly controlled by near-field dilution and saturation state. In lime-based systems, rapid dilution can suppress secondary precipitation (Moras et al., 2022). Shipboard NaOH experiments indicate that precipitation risk is highest just after alkalinity addition, before dilution and air–sea CO₂ uptake lowers the saturation state (Hashim et al., 2025). Recent experiments indicate approach-specific operational ranges: in CaO/Ca(OH)₂ systems, secondary precipitation was absent near $\Omega_A \approx 5$ but occurred above about 7, so rapid dilution below this range is needed to avoid runaway CaCO₃ formation. Similarly, shipboard NaOH additions of 500–2,000 $\mu\text{mol kg}^{-1}$ also produced mineral precipitation on timescales of hours to days (Hashim et al., 2025; Moras et al., 2022).

Currently, there is no universal safe operational threshold for OAE. Available experiments provide only pathway-specific benchmarks. e.g., CO₂-equilibrated additions remain stable at substantially wider alkalinity ranges (e.g., $\Delta\text{TA} < 2,400 \mu\text{mol kg}^{-1}$ in Hartmann et al., 2023; TA up to $\sim 6,500 \mu\text{mol kg}^{-1}$ in Suintner et al., 2024). In contrast, non-CO₂-equilibrated additions become unstable at much lower levels (about $\Delta\text{TA} > 1,000 \mu\text{mol kg}^{-1}$ in Suintner et al., 2024). Similarly, in pH-equilibrated bicarbonate-enriched solutions, stability over at least three months was observed when the increase in overall carbon concentration remained below about 1,000–1,500 $\mu\text{mol L}^{-1}$ (Varliero et al., 2024). This highlights that operational limits depend on feedstock, equilibration state, dilution, and local carbonate chemistry. Exceeding these stability limits can reduce net carbon-removal efficiency through secondary CaCO₃ precipitation and generate environmentally relevant pH excursions. Unequilibrated additions initially raise pH above ambient conditions, whereas runaway precipitation may subsequently return pH toward, or occasionally below, untreated levels (Camatti et al., 2024; Moras et al., 2022; Santinelli et al., 2024). Differences among OAE deployment pathways are especially important for calcifying organisms. Biogenic CaCO₃ production can alter the fate of added alkalinity and reduce OAE efficiency. Precipitation of 1 mol of CaCO₃ removes approximately 2 equivalents of total alkalinity and 1 mol of DIC; by lowering the TA:DIC ratio, enhanced calcification generally shifts seawater carbonate chemistry toward higher pCO₂ and reduces subsequent atmospheric CO₂ uptake. A global modeling study focused on coccolithophores estimated that this feedback could reduce cumulative OAE CO₂ removal through 2,100 by 1.0%–2.8% under moderate alkalinity addition and by 2%–29% under an extreme scenario (Lehmann & Bach, 2025). Calcifier responses are therefore relevant to environmental assessment and, where they materially affect alkalinity budgets, to OAE additionality assessment and supporting MRV (Bednaršek et al., 2025; Ho et al., 2023; Lehmann & Bach, 2025).

Benthic foraminifera warrant particular attention as sediment–water-interface calcifiers that may respond directly in some OAE deployment settings. This imbalance matters because only some OAE pathways are likely to perturb bottom-water or sediment chemistry directly, making benthic receptors such as foraminifera especially relevant in those settings. Benthic foraminifera, although contributing less to global carbonate production than planktonic taxa, play a disproportionately important role in many coastal and shallow-marine environments (Langer, 2008; Schiebel, 2002). Their occurrence at the sediment–water interface makes them important mediators of benthic biogeochemical cycling and carbonate burial. Globally, benthic foraminifera have been estimated to produce about 0.2 Gt CaCO₃ yr^{−1}, equivalent to roughly one-quarter of total foraminiferal carbonate production, and they may account for 5%–55% of carbonate sediment budgets in neritic and reef settings (Girard et al., 2024; Langer, 2008). This combination of carbonate production and direct exposure to bottom-water and

pore-water chemistry makes them particularly well-suited to OAE pathways that perturb benthic habitats. The net effectiveness of OAE therefore depends, in part, on understanding taxon-specific calcification mechanisms and their sensitivity to carbonate-chemistry perturbation (François et al., 2025; Zeebe & Wolf-Gladrow, 2001).

Benthic foraminifera also possess several practical advantages for investigating OAE-driven change. Their short life cycles and rapid community turnover make them sensitive bioindicators of environmental perturbation (Schönfeld et al., 2012). Culture studies also show that reproduction in some larger benthic foraminifera is not strictly dimorphic: trimorphic life cycles with successive schizont generations have been documented in symbiont-bearing taxa such as *Amphistegina* and may help sustain locally adapted populations through repeated asexual reproduction (Dettmering et al., 1998; Hallock & Reymond, 2022). Environmental conditions can also influence reproductive expression, as temperature increased pairing frequency in *Rosalina leei*, reinforcing the need for OAE culture experiments to track life-cycle stage and reproductive mode alongside calcification and survival responses (Nigam & Caron, 2000). Because benthic foraminifera naturally inhabit the sediment surface and shallow infaunal layers, they are well suited to manipulative sediment experiments designed to resolve benthic responses to altered carbonate chemistry. Experimental studies further demonstrate that dominant taxa can rapidly adjust their vertical position after disturbance and that intact assemblages can be maintained for months under laboratory conditions, supporting sediment-based investigations of carbonate-chemistry effects on life-cycle processes (Guilhermic et al., 2023; Haynert et al., 2014). Their biomineralized shells (tests) also preserve morphological and geochemical information relevant to carbonate chemistry and calcification, including isotopic proxies such as $\delta^{13}\text{C}$, $\delta^{18}\text{O}$, and $\delta^{11}\text{B}$ and elemental ratios such as Mg/Ca, Sr/Ca, and B/Ca (Borrelli et al., 2018). These properties make benthic foraminifera useful indicators of OAE-driven changes in bottom-water and pore-water chemistry. They have long been used in paleoceanography and environmental monitoring because their tests record valuable information about marine conditions (Schönfeld et al., 2012; Haynert, 2013; Haynert et al., 2014; Stainbank et al., 2020; Daché et al., 2024; Henry, Boukhary et al., 2025; Henry et al., 2025a). Their fossil record and natural analogs may provide broader context for long-term carbonate-chemistry sensitivity, but in this review their primary value lies in their use as present-day receptors whose calcification, survival, test properties, and geochemical signatures can be measured directly under OAE-relevant conditions (Brown et al., 2011; El-Azabi et al., 2025; Faulkner, 2023; Henry et al., 2025b; Lear et al., 2000, 2010).

Most OAE biological research has focused on pelagic systems, particularly water-column chemistry, planktonic calcifiers, and modeling approaches, whereas benthic and sediment–water interface responses remain poorly constrained (Bach et al., 2019, 2023; Faucher et al., 2025; Gately et al., 2023; Groppelli et al., 2026; Hermoso, 2015; Haynes et al., 2025; Nocera et al., 2025; Traboni et al., 2025). Developing reproducible and comparable workflows for benthic foraminifera is therefore essential for their systematic inclusion in OAE experiments, environmental risk assessment, and supporting monitoring frameworks (Iglesias-Rodríguez et al., 2023). A major gap in OAE research is the absence of standardized methods for quantifying benthic foraminiferal responses in laboratory and mesocosm experiments. At present, there is no common framework for measuring endpoints such as test size, wall thickness, skeletal density, or calcification under elevated alkalinity, which limits direct comparison among studies. Related morphometric approaches have been used under ocean acidification, including buoyant weight, test weight, size-normalized weight or area density, and growth metrics in larger benthic foraminifera (Dissard et al., 2010; Keul et al., 2013; Prazeres et al., 2015), but they have not yet been systematically adapted or standardized for OAE conditions. A similar limitation applies to geochemical approaches: although several proxies are available in foraminiferal research, few have been validated specifically for tracking biomineralization under elevated alkalinity. This dual lack of standardized morphometric protocols and OAE-relevant proxy validation constrains mechanistic interpretation and hampers reproducibility.

This review synthesizes current knowledge and methodological opportunities for assessing the morphological and geochemical responses of calcareous benthic foraminifera to ocean alkalinity enhancement. We distinguish OAE pathways likely to perturb bottom-water or sediment chemistry directly from those whose relevance to benthic foraminifera is more indirect, and we treat natural analogs primarily as hypothesis-generating context rather than direct equivalents of present-day OAE deployments (Eisaman et al., 2023; Figures 1–3). Within this framework, we evaluate morphometric, imaging, and geochemical approaches for their ability to resolve changes in test structure, biomineralization, and physiological response under elevated alkalinity (Figure 1). Our aim is not simply to summarize available techniques, but to connect them into a standardized analytical workflow that supports reproducible experimental design, comparable response variables, and more rigorous interpretation across laboratory, mesocosm, and field studies (Iglesias-Rodríguez et al., 2023; Riebesell et al., 2023).

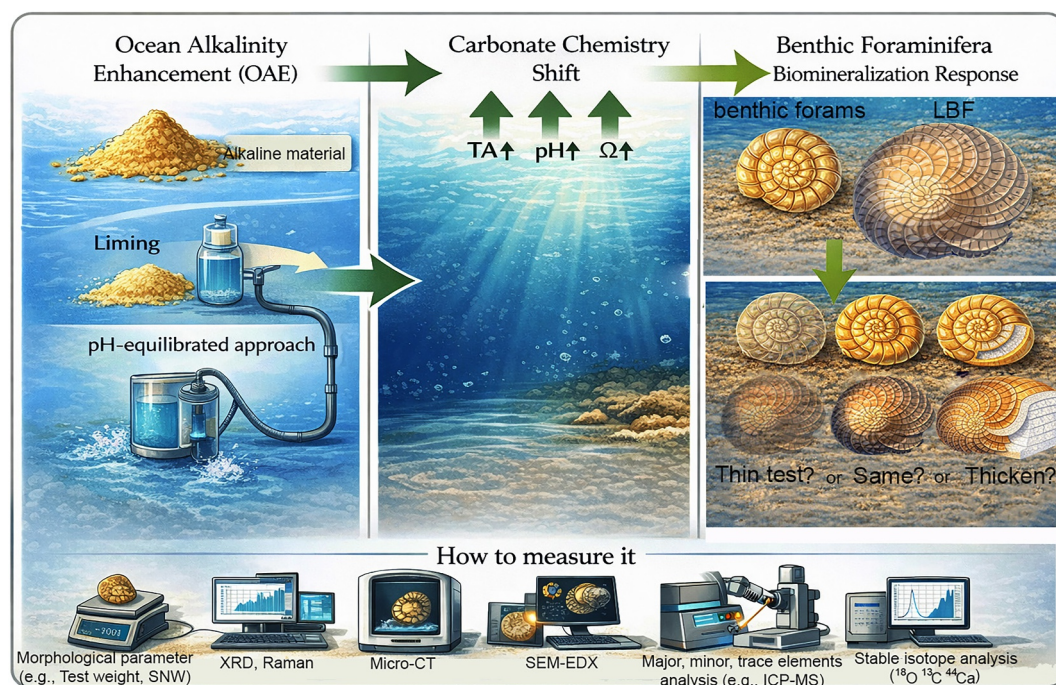


Figure 1. Potential framework for assessing calcareous benthic foraminiferal responses to Ocean Alkalinity Enhancement (OAE). This conceptual model illustrates the progression from alkaline interventions—such as ocean liming—to shifts in carbonate chemistry ($\text{TA}\uparrow$, $\text{pH}\uparrow$, $\Omega\uparrow$) that directly influence biomineralization. Within this framework, calcareous benthic foraminifera serve as critical bioindicators, exhibiting distinct morphological scenarios: they may develop thin tests under stress, remain neutral, or undergo thickening as increased alkalinity reduces the energetic burden of internal pH upregulation. To monitor these responses, a multi-scale analytical toolkit is employed—integrating 3D imaging (micro-CT), mineralogical analysis (XRD, Raman), and a hierarchical four-tier proxy framework—to support environmental assessment and evaluate processes relevant to OAE efficacy.

Ultimately, we assess how benthic foraminiferal responses can inform OAE efficacy and environmental risk assessment and, where calcification feedbacks influence net carbon removal, and environmental monitoring (Bednaršek et al., 2025; Ho et al., 2023).

2. Methodology

Literature was identified through targeted searches of Web of Science, Scopus, and Google Scholar, supplemented by reference-list screening. Search terms combined OAE and carbonate-system manipulation with foraminiferal biology, biomineralization, experimental platforms (culture, microcosms, mesocosms), and analytical endpoints (morphometry, imaging, mineralogy, elemental compositions, and stable isotopes; Figure 1). Studies were included if they reported quantitative morphological or geochemical responses of benthic foraminifera under manipulated carbonate chemistry or provided mechanistic or methodological insights directly applicable to OAE monitoring and interpretation. To establish the mechanistic evidence, base for direct OAE testing, we also included relevant natural analogs. The principal studies meeting these criteria are summarized in Figure 3 (Dissard et al., 2010; Dong et al., 2020; Hall-Spencer et al., 2008; Keul et al., 2013; Kuroyanagi et al., 2021; Mojtahid et al., 2023; Pettit, 2015; Ter Kuile et al., 1989). For each included study, we extracted the experimental context, organismal scope, and measured endpoints, and synthesized the evidence qualitatively to summarize current methodological capabilities, identify uncertainties, and define priorities for future research and monitoring.

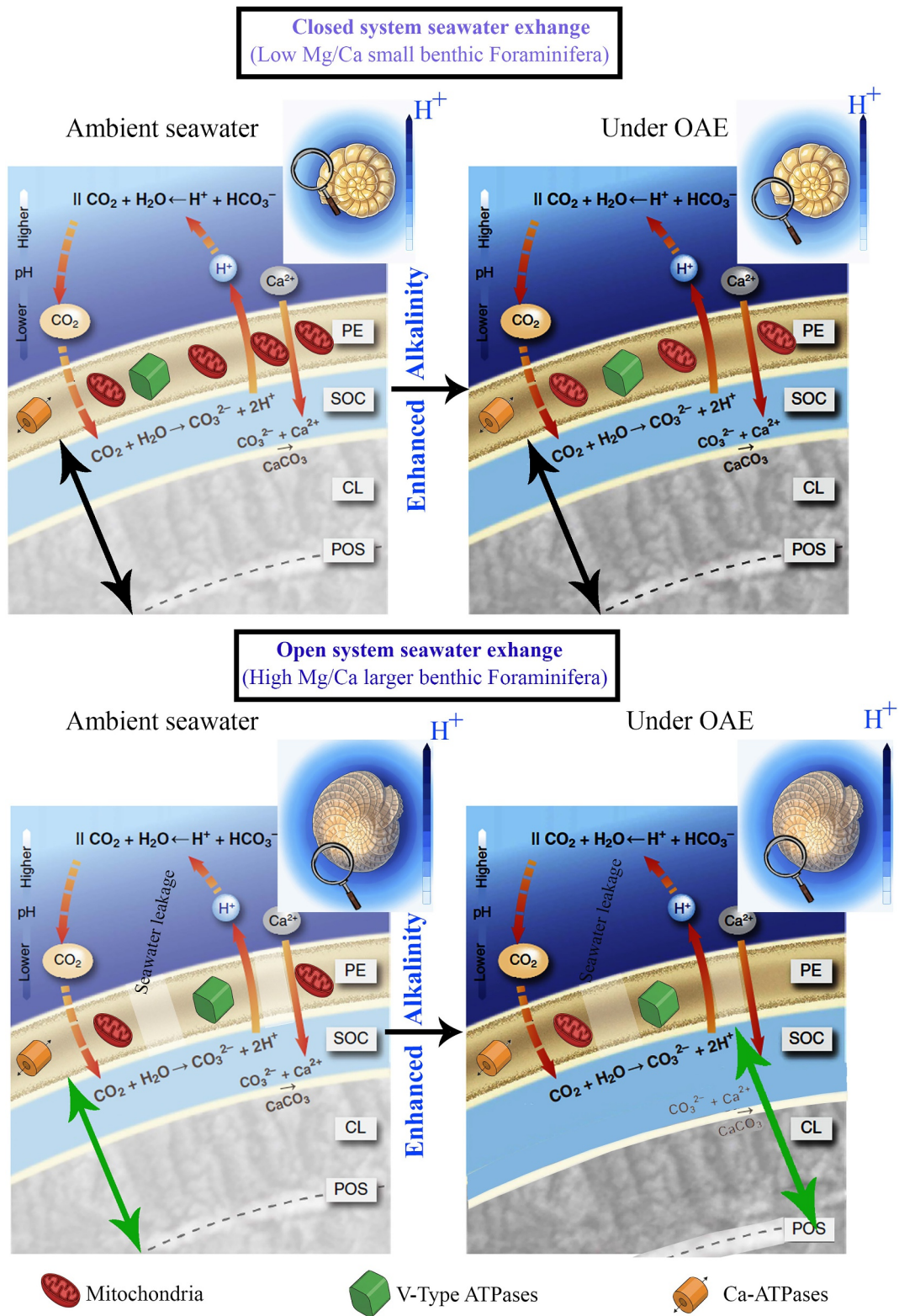


Figure 2.

3. Current Understanding, Limitations, and Future Directions

3.1. Current State of Knowledge

Calcareous benthic foraminifera precipitate calcite (CaCO_3) within a biologically regulated calcifying space rather than passively recording bulk seawater chemistry. Chamber formation involves active control of pH, intracellular transport of Ca^{2+} and dissolved inorganic carbon (DIC), and regulation of carbonate chemistry at the site of calcification (Bentov et al., 2009; de Nooijer, Toyofuku, Kitazato et al., 2009; de Nooijer et al., 2014; François et al., 2025; Glas et al., 2012; Toyofuku et al., 2017). In hyaline taxa, seawater-derived vacuoles can supply Ca^{2+} and DIC, while intracellular amorphous calcium carbonate (ACC) may serve as a transient precursor to crystalline calcite (Bentov et al., 2009; de Nooijer, Toyofuku, Oguri et al., 2009). These processes are coupled to proton removal from the calcifying fluid and proton release to the surrounding seawater, allowing foraminifera to maintain a calcification-site pH above ambient conditions (de Nooijer, Toyofuku, Kitazato et al., 2009; Glas et al., 2012). Carbonic anhydrase (CA), an enzyme that catalyzes the reversible interconversion of CO_2 and HCO_3^- , can accelerate inorganic-carbon supply across this pH gradient and indirectly increase carbonate availability at the calcification site. Inhibition of CA activity strongly reduces calcification in *Amphistegina lessonii* and alters elemental incorporation, demonstrating its importance for both shell formation and test chemistry (de Goeyse et al., 2021, 2024).

This physiological regulation imposes energetic costs that interact with inorganic-carbon availability and external carbonate chemistry. Maintaining an alkaline calcifying fluid requires energy for proton pumping and ion transport, whereas greater inorganic-carbon availability and a higher saturation state can make calcite precipitation thermodynamically more favorable (de Nooijer, Toyofuku, Kitazato et al., 2009, 2014; François et al., 2025; Figure 2). For example, *Ammonia tepida* appears to maintain a relatively closed calcification system associated with stronger pH regulation and greater mitochondrial involvement, whereas the symbiont-bearing *Heterostegina depressa* shows weaker control of the calcifying microenvironment and greater coupling to external carbonate chemistry (François et al., 2025; Figure 2). Symbiont-derived carbon supply may contribute to nonlinear calcification responses under altered carbonate chemistry (François et al., 2025). Dämmer et al. (2023) reported the highest culture-level CaCO_3 production in *Amphistegina lessonii* and *Heterostegina depressa* under moderately elevated pCO_2 , while *A. lessonii* formed thicker chamber walls under intermediate than under ambient or strongly elevated conditions. Thus, benthic foraminiferal calcification is unlikely to respond to pH, DIC, or saturation state in isolation, but instead reflects the combined influence of inorganic-carbon availability, saturation state.

Available experimental evidence is broadly consistent with this interpretation. In *Ammonia tepida*, shell weight decreased with declining carbonate-ion concentration (Dissard et al., 2010; Figure 3). In *Ammonia* sp. (T6), experiments that decoupled pH from (CO_3^{2-}) showed that size-normalized weight and growth were more closely related to carbonate-ion availability than to pH, DIC, total alkalinity, or pCO_2 alone (Keul et al., 2013). *Ammonia* sp. showed limited sensitivity to pH alone, whereas the deep-sea species *Bulimina marginata* and *Cassidulina laevigata* formed fewer new chambers under low-DIC conditions (Mojtahid et al., 2023). Earlier work on larger symbiont-bearing foraminifera also reported enhanced calcification under relatively high-pH conditions, but these studies should be used as mechanistic context rather than treated as direct analogues of present-day OAE exposure (Fujita et al., 2011; Ter Kuile et al., 1989).

In the available studies, metrics of calcification intensity have often been more responsive to carbonate-system change than simple linear-growth measurements. Shell weight, size-normalized weight, density, volume, and chamber-wall thickness can reveal changes that are not apparent from test diameter or surface-area growth alone (Prazeres et al., 2015; Kuroyanagi et al., 2021; Dämmer et al., 2023; Figure 3). In *Amphistegina lessonii*, reduced pH lowered buoyant weight and inner-chamber density without strongly affecting lateral surface-area growth,

Figure 2. Mechanistic model of benthic foraminiferal biomineralization and energetic shifts under Ocean Alkalinity Enhancement (OAE). This model illustrates how elevating seawater alkalinity ($\text{TA}\uparrow$) and saturation ($\Omega\uparrow$) may alleviate the metabolic burden of internal pH upregulation—driven by mitochondrial ATP and proton pumping—thereby potentially promoting thicker or denser tests in species like larger benthic foraminifera. It contrasts “closed” systems (e.g., *Ammonia* sp.), which maintain stable calcification through high energy investment, with “open” systems (e.g., *Heterostegina* sp.) that are more sensitive to external chemical shifts. Closed systems (e.g., *Ammonia* sp.) are predicted to remain relatively stable because calcification is limited by biological pumping rates rather than external Ω (black double arrows). Open systems (e.g., *Heterostegina* sp.) are more responsive to seawater chemistry; higher Ω under OAE may lower precipitation costs and allow greater calcification and wall thickening (green double arrows). Modified after Toyofuku et al. (2017) and François et al. (2025).

Study (Author, Year)	Species / Community	System	Manipulation Type	Range (pH, [CO ₃ ²⁻], Ω _{calcite})	Timescale (exposure / response)	Main Response (Shell Weight, SNW, Growth, Density, Survival, Assemblage)	Inferred Driver
Dissard et al. (2010)	<i>Ammonia tepida</i>	Culture	CO ₂ (Decoupled, 120/2000 ppm)	Large diff. in [CO ₃ ²⁻], Ω	1.5 mo; end-point	↓ Shell weight (with ↓ [CO ₃ ²⁻])	[CO ₃ ²⁻]
ter Kuile et al. (1989)	<i>Amphistegina lobifera</i>	Culture	pH	pH 8.2–8.9	48 h; 12–24 h, clearer 24–48 h	↑ Calcification efficiency	pH
	<i>Amphisorus hemprichii</i>	Culture	pH	pH > 8.4	48 h, over 48 h	↑ Calcification markedly	pH
Keul et al. (2013)	<i>Ammonia</i> sp.	Culture	Decoupled (TA vs Stable-pH)	pH 7.6–8.32; Ω 0.5–13.8	59–96 d; end-point	↑ SNW & Growth (with [CO ₃ ²⁻])	[CO ₃ ²⁻]
Kuroyanagi et al. (2021)	<i>Amphisorus kudakajimensis</i>	Culture	pH	pH 7.7–8.3	10 wk; 6–8 wk growth, 10 wk end-point	↑ Weight, Volume, Density (with pH)	pH / Ω
Pettit (2015)	Community (LBF)	Field Seep	CO ₂ Gradient	pH 8.1 → ~7.7	Natural seep exposure ; assemblage sampled	↓ Abundance/Diversity; Assemblage shift	Ω / pH
Hall-Spencer (2008)	Community	Field Seep	CO ₂ Gradient	pH 8.1 → 6.6	Natural seep exposure ; 2006–2007 surveys	↓ Calcareous taxa; Agglutinated dominate	Ω / pH
Mojtahid et al. (2023)	<i>Ammonia</i> sp.	Culture	Decoupled (DIC/TA)	pH 7.6–8.4; DIC 879–7131	~45 d; end-point	— Survival/Growth (Neutral)	Resilience
Mojtahid et al. (2023)	<i>Bulimina</i> / <i>Cassidulina</i>	Culture	Decoupled (Low DIC)	Low DIC (879 μmol kg ⁻¹)	~45 d; end-point	↓ Calcification	Carbonate Availability
Dong et al. (2020)	Community (Intertidal)	Microcosm	pH	pH 6.5–8.5	4 mo; end-point	↑ Abundance & Proportion	pH

Main Response: Green = Positive (↑), Red = Negative (↓), Grey = Neutral (—)

Figure 3. A comparative synthesis of benthic foraminiferal calcification and survival across carbonate chemistry regimes, integrating culture, field seep, and microcosm studies. Results indicate that acidified or low-DIC conditions commonly reduce shell weight and community diversity (red), whereas elevated pH and carbonate availability generally promote neutral to positive calcification responses (gray–green). These patterns underscore species-specific resilience and identify carbonate ion concentration as a key control on foraminiferal physiological performance. Timescale denotes total exposure duration and, where available, approximate response timing; h = hours, d = days, wk = weeks, mo = months, end-point = assessed at the end of the experiment, and natural seep gradient = field assemblages sampled along persistent CO₂-seep conditions rather than controlled-duration exposures.

while micro-CT resolved changes in chamber-wall thickness that would have remained undetected using linear measurements alone (Dämmer et al., 2023; Prazeres et al., 2015). *Amphisorus kudakajimensis* likewise showed coordinated declines in shell weight, volume, and density under acidified conditions (Kuroyanagi et al., 2021). At the assemblage level, microcosm and shallow-water CO₂-seep studies report lower representation of calcareous taxa and greater prominence of agglutinated forms under more corrosive conditions, although these natural analogues also integrate ecological and geochemical influences beyond carbonate chemistry alone (Dias et al., 2010; Dong et al., 2020; Hall-Spencer et al., 2008; Pettit, 2015).

Taken together, available studies indicate that calcification metrics in several calcareous benthic foraminiferal taxa are higher under less corrosive, more carbonate-rich conditions, although the magnitude and direction of response vary with taxon, life strategy, and the carbonate-system variable being manipulated. Moderate alkalinity enhancement could reduce the energetic cost of maintaining an alkaline calcifying fluid in some species particularly larger benthic foraminifera (Figure 2); yet this remains a testable hypothesis rather than a general prediction. Its relevance is greatest for OAE pathways that directly modify bottom-water or pore-water chemistry; surface-water interventions involving little benthic exposure may produce limited or delayed responses.

3.2. Integrated Analytical Framework for OAE-Related Foraminiferal Responses

3.2.1. Framework Overview

The three-tier framework progresses from high-throughput growth screening in Tier 1 to size-normalized calcification measurements in Tier 2 and structural or mineralogical attribution in Tier 3 (Figure 4). Its end-points derive from ocean-acidification and decoupled carbonate-system studies used as mechanistic inverse analogs for direct OAE testing. Where chemical attribution is required, elemental and isotopic analyses can relate observed changes to carbonate-system perturbation, feedstock chemistry, biomineralization, or environmental overprints.

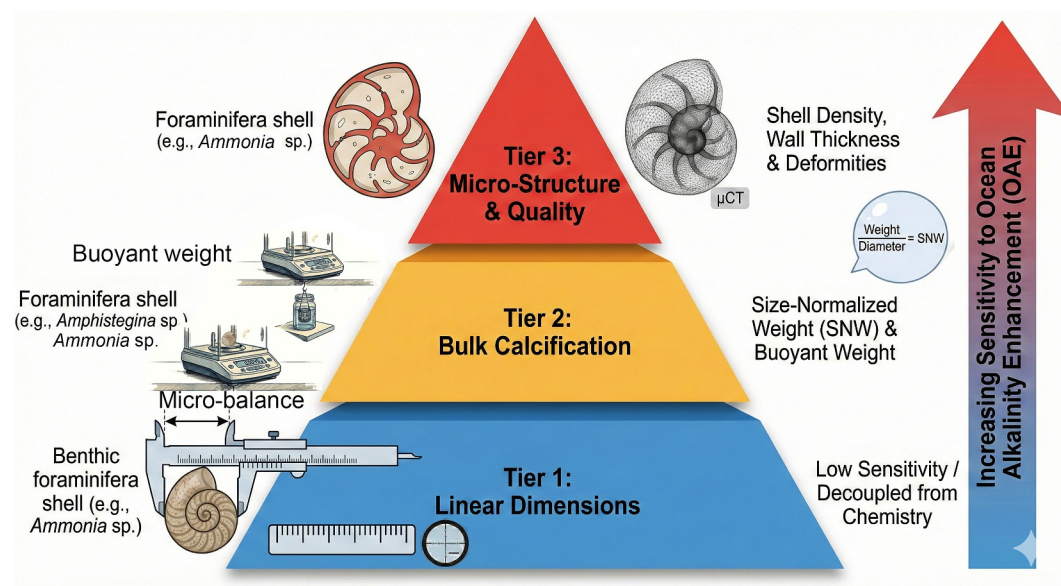


Figure 4. Proposed three-tier morphological–structural framework for assessing benthic foraminiferal responses under OAE-relevant carbonate-chemistry perturbations (Dissard et al., 2010; Dong et al., 2020; Keul et al., 2013; Kuroyanagi et al., 2021; Prazeres et al., 2015). A conceptual stratification of morphological metrics based on their sensitivity to carbonate chemistry perturbations, derived from culture and microcosm experiments. (bottom) Tier 1: Linear dimensions (e.g., maximum diameter), are the screening metrics. Studies on *Amphistegina lessonii* indicate that lateral growth can be decoupled from calcification stress, maintaining extension rates even while shell mass decreases (Prazeres et al., 2015). These features are often driven more by temperature than by saturation state (Kuroyanagi et al., 2021). (middle) Tier 2: Bulk calcification metrics, such as Size-Normalized Weight (SNW) and Buoyant Weight, show mass-based quantification. SNW positively correlates with carbonate ion concentration (CO_3^{2-}) in *Ammonia* sp., attribution to wall thickness or skeletal density requires Tier 3 analysis (Dissard et al., 2010; Keul et al., 2013; Prazeres et al., 2015). (top) Tier 3: Micro-structural and quality metrics represent microstructural/mineralogical attribution. Utilizing Micro-CT, this tier detects cryptic alterations such as 3D density loss and inner chamber volume reduction (Kuroyanagi et al., 2021). It also includes deformity frequency, which increases significantly under chemical stress (Dong et al., 2020).

3.2.2. Tier 1: Linear Dimensions and Growth Responses

Tier 1 provides a rapid, high-throughput screen of whether OAE exposure alters gross test development. Maximum test diameter, projected area, chamber addition, and linear or surface-area growth can be measured across many specimens and treatments, preferably using standardized, non-destructive imaging protocols (Dämmer et al., 2023; Keul et al., 2013; Prazeres et al., 2015). Gross abnormalities may be noted during screening (Dong et al., 2020), but systematic assessment of test deformities is undertaken in Tier 3. Tier 1 measurements should not be treated as direct estimates of calcification, because linear growth may remain unchanged despite changes in test weight, density, or wall thickness (Dämmer et al., 2023; Kuroyanagi et al., 2021; Prazeres et al., 2015).

3.2.3. Tier 2: Bulk Calcification Responses

Tier two quantifies mass-based calcification using test weight, size-normalized weight or area density, and buoyant weight, which can reveal responses not apparent from linear or surface-area growth alone (Dissard et al., 2010; Keul et al., 2013; Prazeres et al., 2015). Because normalization procedures vary among taxa and studies, test mass should be normalized using an explicitly defined and taxon-appropriate size metric rather than a universal formula.

3.2.4. Tier 3: Microstructure, Mineralogy and Test Quality

Tier 3 uses complementary microstructural, mineralogical, and compositional methods to explain mass-based responses detected in Tier 2 and to investigate test alteration, particle adhesion, or secondary mineral formation where these are primary study questions (Figures 4 and 5). Bulk measurements of Tier 2 cannot distinguish

Analytical Toolbox for Benthic Foraminiferal Biomineralization: Methods vs. Diagnostic Capabilities

	Polymorph ID (Calcite/Aragonite)	Crystallinity / Structural Order	Porosity / Shell Ultrastructure	Test Density / Integrity	Elemental Mapping (e.g., Mg Zoning)	Seawater pH/Carbonate Proxy	Diagenesis Risk / Alteration
X-ray Diffraction (XRD)	✓ Quantify Phases (e.g., Mg-calcite)	✓ Crystallinity Shifts (e.g., FWHM of 104 reflection)					
Raman Spectroscopy	✓ Identify Polymorphs	✓ Lattice Vibrations, ACC Precursors, Stress					
SEM (Scanning Electron Microscopy)			✓ Pits, Overgrowth, Deformation ✓ Pores of test (size, density, porosity)	✓ Visual Structural Integrity			
Micro-CT (Micro-computed tomography)			✓ 3-D test volume, chamber architecture, wall thickness, internal voids/porosity	✓ Structural integrity; apparent skeletal density			
SEM-EDX (Energy-Dispersive X-ray Spectroscopy)					✓ Qualitative/Semi- Quant Mapping (Ca, Mg, B, S)		
EPMA (Electron Probe Microanalysis)					✓ Detailed Quantitative Mapping, Trace Partitioning (Mg/Ca, Sr/Ca)		
Major/Minor/Trace Elements (e.g., Mg, Sr, Na, Fe, S, K, B, Ba)						✓ Seawater Chemistry, Biomineralization Insights, U/Ca (ca. ion activity), Si/Ca (Inverse CO_3^{2-}), Li/Ca (HCO_3^-), Sat. state, Na/Ca (Plume Tracer)	✓ Diagenetic Indicators (Fe, Mn), Al/Ca (Cleaning Efficacy/Contaminants)
Stable Isotopes (e.g., $\delta^{13}\text{C}$, $\delta^{18}\text{O}$, $\delta^{15}\text{N}$, $\delta^{44/40}\text{Ca}$)						✓ Calcification Dynamics, pH ($\delta^{18}\text{B}$), $\delta^{44/40}\text{Ca}$ (OAE Feedstock Tracing)	✓ Diagenetic Indicators ($\delta^{18}\text{O}$, $\delta^{13}\text{C}$)

✓ Green Checkmark = Primary Detection Capability / Strong Indicator

Figure 5. Analytical toolbox for benthic foraminiferal biomineralization: Methods versus diagnostic capabilities. This integrated matrix categorizes established analytical techniques to detect physiological and structural shifts in benthic foraminifera under environmental perturbations like Ocean Alkalinity Enhancement (OAE).

whether changes in test mass arise from wall thickness, skeletal density, chamber volume, dissolution, or secondary deposition, and they may miss localized deformation or structural damage.

Micro-CT and SEM provide complementary three- and two-dimensional evidence of structural change. Micro-CT non-destructively quantifies test volume, chamber architecture, and wall thickness and, when combined with test mass and standardized image segmentation, can estimate apparent skeletal density (Figures 4 and 5). In OAE experiments, these measurements can help determine whether a bulk-calcification response reflects altered chamber volume, wall thickness, the distribution of mineralized material, or test integrity. SEM complements this analysis by resolving surface preservation, pore morphology, lamellar structure, dissolution, deformation, and overgrowth at finer spatial scales (Guamán-Guevara et al., 2019). Focused-ion-beam SEM observations further show that foraminiferal tests comprise layered biocalcite separated by organic interfaces and nanoscale voids, providing a microstructural basis for interpreting OAE-related changes in wall integrity and mineral deposition (Nagai et al., 2018). Ocean-acidification studies demonstrate the value of this combination in application to OAE: surface-area growth may remain comparatively stable even when buoyant weight, test density, volume, or wall thickness changes (Dämmer et al., 2023; Kuroyanagi et al., 2021; Prazeres et al., 2015).

XRD and Raman spectroscopy complement microstructural analysis by resolving mineral phase and crystallization pathway. XRD detects bulk CaCO_3 phases and evaluates crystal order from phase-specific peak positions and broadening. In OAE experiments, XRD can test whether foraminiferal tests retain their expected primary mineralogy. It also determines whether structural or mass changes are accompanied by altered crystal order (Bassinot et al., 2004; Cotton et al., 2020) or secondary CaCO_3 phases, which may form above analytical detection limits due to high saturation states or OAE feedstocks. Because conventional powder XRD often requires pooled material and provides limited spatial information, it could be interpreted alongside spatially resolved mineralogical and compositional methods, particularly Raman spectroscopy, SEM-EDS, and EPMA. Raman spectroscopy complements this bulk assessment through non-destructive analysis of mineral identity, lattice disorder, and poorly crystalline carbonate phases, including ACC (Kim et al., 2021). It can distinguish

CaCO_3 polymorphs and map crystal disorder and Mg-related spectral heterogeneity across chamber walls and growth structures (Alves et al., 2023; DeCarlo et al., 2019; Dubicka et al., 2023; Wehrmeister et al., 2009). Raman can therefore test whether elevated alkalinity modifies the distribution, persistence, or conversion of ACC into crystalline calcite during shell formation (Dubicka et al., 2023, 2025; Mass et al., 2017).

SEM-EDS and EPMA provide the compositional attribution needed to interpret these structural and mineralogical observations. SEM-EDS supports rapid qualitative or semi-quantitative mapping, whereas EPMA provides more robust quantitative elemental mapping and lower detection limits than SEM-EDS for many elements. In OAE experiments, these methods can identify chemically distinct residual feedstock particles and Mg-, Fe-, or Si-rich coatings. Distinguishing primary test calcite from compositionally similar secondary CaCO_3 precipitates requires integration with spatial, textural, and mineralogical evidence from SEM, Raman, or XRD. This distinction is important because externally deposited material could increase test mass or alter surface appearance without representing enhanced foraminiferal calcification. Elemental mapping helps establish whether the observed response primarily reflects altered biomineralization or external mineralogical overprinting. It therefore provides the transition from the morphological–structural tiers to the geochemical proxy framework.

3.3. Application, Usability, and MRV Relevance of the Three-Tier Framework

The proposed framework is modular and question-driven; individual studies need not apply every tier. It addresses four sequential questions: does OAE exposure alter gross foraminiferal test development; does it change test carbonate mass; what structural or mineralogical process underlies the response; and does the signal reflect biomineralization rather than dissolution, adhered feedstock, or secondary mineral precipitation? Laboratory experiments provide the most controlled setting for calibrating species-specific responses to alkalinity source, treatment intensity, equilibration state, exposure duration, and interacting environmental variables. Experimental designs should include replication, standardized endpoints, multilevel treatment gradients, and pathway-specific secondary-precipitation thresholds (Dupont & Metian, 2023; Iglesias-Rodríguez et al., 2023). Applied modularly, Tier 1 screens test development, Tier two quantifies mass-based responses, and Tier 3 resolves their structural or mineralogical basis. Tier 3 specimens should be selected using predefined, balanced criteria representing controls and all treatment levels.

Mesocosm and field applications require greater attention to ecological complexity and exposure attribution. Benthic mesocosms are especially relevant to particulate OAE because feedstocks may alter sediment properties, pore-water chemistry, trace-metal availability, and habitat conditions (Riebesell et al., 2023). Field studies should be limited to settings with plausible benthic exposure and include pretreatment baselines, appropriate reference areas, and concurrent measurements of bottom-water and pore-water carbonate chemistry (Cyronak et al., 2023). Temporal attribution further requires living or recently active specimens, newly formed foraminiferal test material, or other evidence that the response developed during exposure.

The three-tier framework can inform the monitoring component of MRV and constrain additionality-related feedbacks where benthic calcification or secondary precipitation affects OAE efficiency. Precipitation of CaCO_3 reduces the atmospheric CO_2 uptake attributable to alkalinity addition (Ho et al., 2023; Schulz et al., 2023). Scaling these observations to benthic carbonate-production fluxes would additionally require individual production rates, species composition and specimen abundance, life-stage composition, population turnover, and adequate spatial and temporal coverage. The framework can therefore identify and constrain processes relevant to OAE additionality, but it cannot independently quantify their ecosystem-scale effect. Assemblage composition provides a complementary ecological indicator of environmental change (Carneiro et al., 2026; Koukousioura et al., 2011; Murray, 2006; Schönfeld et al., 2012); combined with the three-tier framework, it offers standardized biological and mineralogical evidence for the monitoring component of broader OAE assessment.

3.4. Elemental and Isotopic Framework

To synthesize proxy behavior under OAE, Table 1 groups available geochemical indicators into four functional tiers: primary carbonate-system proxies, feedstock- or major-ion tracers, species-sensitive biomineralization proxies, and contextual or quality-control proxies.

Table 1
Proposed Four-Tier Functional Framework for Geochemical Proxies Relevant to OAE Interpretation in Benthic Foraminifera

Geochemical proxy	Potential interpretation	Application to OAE scenarios	References
U/Ca	Carbonate-ion/saturation-state proxy, largely independent of pH.	Promising local indicator of sustained carbonate-system change in benthic settings, provided cleaning and redox screening are applied.	Russell et al. (1996), Raitzsch et al. (2011), Levin et al. (2015)
$\delta^{11}\text{B}$	pH proxy reflecting seawater borate composition; epifaunal and infaunal taxa record different microhabitats.	Potentially valuable for detecting local pH elevation in benthic settings directly exposed to alkalinity perturbation; requires species- and habitat-specific calibration and is best used in a multi-proxy framework.	Rae et al. (2011), Clarkson et al. (2015)
Li/Ca	Promising but still insufficiently validated indicator of carbonate saturation.	Potential supporting proxy for local saturation-state change; currently indirect and not yet validated in direct OAE exposure experiments.	Lear et al. (2010), Dawber and Tripathi (2012)
Na/Ca	Contextual major-ion proxy influenced more by seawater Ca^{2+} /salinity relationships than by salinity alone.	Potentially useful in pathway-specific settings that measurably alter Ca^{2+} /salinity relationships; not a general OAE plume tracer.	Mezger et al. (2016), Pachó et al. (2024)
K/Ca	Contextual major-ion proxy for seawater K^{+} .	May help identify pathway-specific major-ion perturbations or provide a background chemical reference in multi-proxy interpretation.	Pachó et al. (2024)
$\delta^{44}/^{40}\text{Ca}$	Specialized tracer of seawater Ca isotopic composition.	Relevant mainly to calcium-based deployment pathways that measurably alter local Ca isotope composition; not a general OAE monitoring proxy.	Griffith and Fantle (2020), Fantle and DePaolo (2007)
Mg/Ca	Species-sensitive proxy influenced by temperature, seawater Ca^{2+} , saturation state, and biomineralization controls.	Must be interpreted cautiously because carbonate-system changes can confound its conventional temperature signal; not a direct stand-alone OAE proxy.	Segev and Erez (2006)
S/Ca	Mechanistically promising but species-sensitive carbonate-chemistry proxy; directionality remains debated across taxa.	May help track carbonate-system change and biologically regulated calcification under elevated alkalinity, but requires species-specific calibration and should not yet be treated as universally transferable.	van Dijk et al. (2017, 2019), Karancz et al. (2024)
Sr/Ca Ratio	Species-sensitive proxy reflecting internal calcifying-fluid regulation.	Should be used cautiously and only with species-specific calibration, because responses depend on how elevated alkalinity alters the regulated calcification environment rather than external seawater chemistry alone.	Rosenthal et al. (2006), Mojtabid et al. (2023), Jia et al. (2024);
B/Ca Ratio	Complementary but species-dependent boron proxy, less robust than $\delta^{11}\text{B}$ as a stand-alone carbonate-chemistry indicator.	Best interpreted alongside boron isotopes and other carbonate-system proxies rather than as an independent indicator of OAE response.	Berry (1998), Petit (2015)
Cd/Ca & Zn/Ca	Nutrient and preservation context proxies with limited secondary sensitivity to carbonate saturation.	Useful mainly as contextual indicators for separating nutrient or preservation effects from primary biomineralization signals; not primary OAE proxies.	Marchitto et al. (2000, 2002), Rosenthal et al. (2006)
Mn/Ca, U/Mn, and Al/Ca	Redox overprint and contamination screening proxies.	Used to identify authigenic coatings, redox overprints, and residual clay contamination, thereby increasing confidence that primary carbonate-system proxies reflect benthic exposure to alkalinity perturbation.	Barker et al. (2003), Thibault de Chanvalon et al. (2023), Boiteau et al. (2012)
$\delta^{13}\text{C}$	Contextual proxy for DIC source, ventilation, remineralization, and microhabitat effects.	Helps distinguish carbonate-system perturbations from changes in DIC source, ventilation, or benthic remineralization when interpreted alongside more direct proxies such as $\delta^{11}\text{B}$, U/Ca, or S/Ca.	Schmittner et al. (2017), Toyofuku et al. (2017), Hoogakker et al. (2024)

Table 1
Continued

Geochemical proxy	Potential interpretation	Application to OAE scenarios	References
$\delta^{18}\text{O}$	Contextual proxy reflecting bottom-water temperature and seawater $\delta^{18}\text{O}$.	Used mainly as a quality-control proxy to identify unintended hydrographic variability, diagenetic overprinting, or secondary precipitation rather than as a direct recorder of alkalinity addition.	Bemis et al. (1998), Marchitto et al. (2014)

Note. Tier 1 comprises the most mechanistically grounded candidate carbonate-system proxies, including U/Ca and $\delta^{11}\text{B}$, with Li/Ca retained as a promising but less well validated saturation-state indicator. Tier 2 comprises pathway-specific feedstock or major-ion tracers, such as Na/Ca and K/Ca, and where relevant $\delta^{44}/^{40}\text{Ca}$, that may help identify local changes in seawater composition associated with particular OAE deployment modes. Tier 3 comprises species-sensitive biomineralization proxies, including Mg/Ca, Sr/Ca, S/Ca, and B/Ca, whose behavior is strongly influenced by calcifying-fluid regulation, growth, and other vital effects. Tier 4 comprises contextual and quality-control proxies, including $\delta^{13}\text{C}$, $\delta^{18}\text{O}$, Cd/Ca, Zn/Ca, Mn/Ca, U/Mn, and Al/Ca, which help distinguish primary OAE-related signals from nutrient, redox, contamination, hydrographic, or diagenetic overprints. Tiers reflect current interpretive role and level of confidence under OAE, rather than a universal ranking of proxy sensitivity. See table for relevant references.

Among trace-element proxies, U/Ca is one of the more mechanistically grounded indicators of carbonate-system change in benthic foraminiferal calcite. Experimental and core-top studies show that uranium incorporation generally decreases as seawater $[\text{CO}_3^{2-}]$ and calcite saturation state increase, reflecting the greater stability of dissolved uranyl-carbonate complexes under more alkaline conditions (Keul et al., 2013; Levin et al., 2015; Raitzsch et al., 2011; Russell et al., 1996). In cultured *Ammonia* sp., the uranium partition coefficient declines systematically with rising (CO_3^{2-}) , independent of pH, supporting the interpretation of U/Ca as a proxy for carbonate ion availability rather than pH alone (Keul et al., 2013). Comparable negative correlations between U/Ca and carbonate saturation have also been reported in deep-sea benthic taxa such as *Planulina wuellerstorfi* and *Cibicidoides mundulus* (Raitzsch et al., 2011; Russell et al., 1996). In the context of OAE, this makes U/Ca a promising candidate for tracking alkalinity-driven shifts in carbonate chemistry, especially in settings where bottom-water or pore-water (CO_3^{2-}) is expected to change directly. However, its application under OAE requires careful screening and calibration. Post-depositional coatings enriched in uranium and manganese can artificially elevate U/Ca, particularly in reducing sediments, so rigorous cleaning and exclusion of specimens with elevated Mn/Ca are essential to isolate lattice-bound uranium (Chen et al., 2017). In addition, interspecific differences in uranium partitioning mean that U/Ca should not be transferred uncritically among taxa (Keul et al., 2013; Raitzsch et al., 2011). Because some OAE pathways may also modify benthic redox conditions, it is important to distinguish primary biomineralization signals from secondary authigenic U enrichment (Boiteau et al., 2012). Used in this way, and ideally alongside complementary carbonate-system proxies such as S/Ca, benthic foraminiferal U/Ca may help evaluate whether alkalinity enhancement produces detectable local increases in carbonate ion availability over deployment-relevant timescales in settings where bottom-water or pore-water chemistry is modified directly. In this context, such changes may provide indirect evidence that added alkalinity is being retained locally in geochemically effective form.

$\delta^{11}\text{B}$ remains one of the most promising proxies for tracking pH change under OAE. Its incorporation is linked to the acid-base equilibrium between boric acid and borate in seawater, with foraminifera preferentially incorporating the borate species into calcite, so that test $\delta^{11}\text{B}$ reflects ambient pH (Foster & Rae, 2016; Rae et al., 2011). Supporting natural-analog evidence from CO_2 -seep settings shows that $\delta^{11}\text{B}$ in *Amphistegina lessonii* decreases with declining pH, whereas B/Ca and Ba/Ca vary more strongly among species and show less direct coupling to carbonate chemistry (Pettit, 2015). Epifaunal benthic taxa such as *Cibicidoides wuellerstorfi*, *Cibicidoides mundulus*, and *Planulina ariminensis* commonly record values close to the calculated $\delta^{11}\text{B}$ of seawater borate at bottom-water pH, whereas infaunal taxa more often reflect pore-water pH and sedimentary respiration effects (Clarkson et al., 2015; Rae, 2018; Rae et al., 2011). In the context of OAE, $\delta^{11}\text{B}$ is therefore potentially valuable for detecting local pH elevation in benthic settings directly exposed to alkalinity perturbation. However, species-specific vital effects, habitat differences, and incomplete calibration across taxa still limit its transferability. $\delta^{11}\text{B}$ is thus best applied as a calibrated component of a multi-proxy framework, rather than as a universal stand-alone indicator of OAE response.

Li/Ca is a potentially useful proxy for carbonate saturation in benthic foraminiferal calcite. Existing studies indicate that Li/Ca increases with enhanced calcite saturation and carbonate ion availability, supporting the interpretation that Li incorporation is sensitive to bottom-water carbonate chemistry rather than temperature alone (Dawber & Tripathi, 2012; Lear et al., 2010; Lear & Rosenthal, 2006). In particular, paired Mg/Ca–Li/Ca approaches suggest that Li/Ca may help isolate the saturation-state component of test chemistry where Mg/Ca remains more strongly influenced by temperature (Lear et al., 2010). In the context of OAE, this implies that Li/Ca could prove useful for assessing whether alkalinity enhancement produces detectable increases in carbonate saturation in benthic settings directly exposed to modified bottom-water chemistry. Li/Ca should therefore be regarded as a promising proxy, best applied alongside complementary carbonate-system indicators rather than as a stand-alone measure.

Na/Ca and K/Ca are better viewed as contextual major-ion proxies than as primary indicators of benthic foraminiferal response to OAE. Although Na/Ca has historically been linked to salinity (Mezger et al., 2016; Wit et al., 2013), recent calibration work on the larger benthic foraminifer *Amphistegina lessonii* suggests that Na incorporation is influenced more strongly by seawater Ca^{2+} than by salinity itself, while remaining largely insensitive to temperature (Pacho et al., 2024). This makes Na/Ca potentially relevant for OAE pathways that measurably modify seawater Ca^{2+} /salinity relationships, such as calcium-based dissolution scenarios, but probably less useful as a general OAE proxy across all deployment modes. In the same study, K/Ca behaved as a more direct recorder of seawater K^+ and appeared comparatively insensitive to Ca^{2+} and temperature (Pacho

et al., 2024). In this context, Na/Ca and K/Ca may be useful as supporting tracers of feedstock-related changes in seawater major-ion composition, but their applicability to OAE remains strongly pathway- and site-specific.

The Ca isotopic composition of benthic foraminiferal calcite ($\delta^{44/40}\text{Ca}$) is controlled primarily by the isotopic composition of seawater Ca and by species-specific biological fractionation during calcification, with benthic tests typically offset to lower values than seawater (Griffith & Fantle, 2020; Gussone et al., 2003; Gussone & Filipsson, 2010; Gussone & Heuser, 2016). Because Ca isotopes are generally less sensitive to post-depositional overprinting than many element ratios, $\delta^{44/40}\text{Ca}$ may provide useful complementary information where carbonate dissolution, recrystallization, or calcium-source perturbation is a concern (Fantle & DePaolo, 2007; Fantle & Higgins, 2014). In the context of OAE, however, its applicability is likely to be limited to pathways that measurably modify seawater Ca isotopic composition, such as dissolution of calcium-bearing minerals or carbonates, rather than alkalinity additions that do not substantially perturb Ca supply. Furthermore, the vast global inventory and long residence time of seawater Ca (~ 1 Myr) heavily buffer the ocean's overall isotopic composition (Fantle & Tipper, 2014). Therefore, while local seawater chemistry responds immediately (within hours to days) to an OAE calcium addition, the rapid dilution and modest size of these short-term perturbations mean that $\delta^{44/40}\text{Ca}$ is unlikely to function as a general OAE monitoring proxy. Accordingly, $\delta^{44/40}\text{Ca}$ is best reserved as a specialized local tracer for calcium-bearing deployment pathways and interpreted alongside more direct carbonate-system proxies such as $\delta^{11}\text{B}$, U/Ca, or B/Ca.

Mg/Ca and Sr/Ca are among the most widely used element-to-calcium ratios in benthic foraminiferal calcite, but both are strongly species-dependent. Mg/Ca is classically used as a bottom-water temperature proxy, yet experimental work shows that it may also respond to seawater Ca^{2+} concentration, calcite saturation state, and broader carbonate-system conditions in some taxa (Elderfield et al., 2006; Lear et al., 2000; Raitzsch et al., 2010; Rosenthal et al., 2006). In *Ammonia tepida*, however, no measurable Mg response to (CO_3^{2-}) was observed under pCO_2 manipulation (Dissard et al., 2010). Culture studies further show contrasting responses: Mg incorporation decreases with increasing Ca^{2+} and Ω_{calcite} in the low-Mg species *A. tepida*, whereas in the high-Mg species *Heterostegina depressa* Mg/Ca changes little but Sr partitioning increases with Ω_{calcite} (Raitzsch et al., 2010). These patterns indicate that Mg and Sr incorporation reflect both external carbonate chemistry and biological regulation of the calcifying fluid (de Nooijer et al., 2014). Low-Mg taxa likely reduce Mg incorporation through stronger physiological control, whereas high-Mg taxa appear more responsive to ambient seawater chemistry (Segev & Erez, 2006; Raitzsch et al., 2010; Table 1). Because current OAE applications involve short-term releases and field trials rather than long-term geological timescales, tracking foraminiferal Mg/Ca in these contexts is not intended for temperature reconstruction. Instead, it serves as a direct, short-term sensor of altered seawater chemistry. In the context of OAE, Mg/Ca and Sr/Ca should therefore not be interpreted as simple responses to pH, DIC, or saturation state alone. Their application under elevated alkalinity requires species-specific calibration and explicit consideration of how external seawater chemistry is translated into the regulated calcifying fluid. In pathways using Mg-rich feedstocks such as $\text{Mg}(\text{OH})_2$, local seawater Mg/Ca and precipitation conditions may also be transiently modified, but these effects are most relevant to deployment settings with direct benthic exposure (Hartmann et al., 2023; Pacho et al., 2024).

Sr/Ca also shows species-specific sensitivity to carbonate-system change, but its response appears to depend strongly on how external conditions are translated into the regulated calcifying fluid. In some cultured taxa, including *Heterostegina depressa* and *Ammonia tepida*, Sr uptake increases with higher Ω_{calcite} and (CO_3^{2-}) (Dissard et al., 2010; Raitzsch et al., 2010). However, Jia et al. (2024) showed that in low-Mg benthic species such as *Cibicides wuellerstorfi* and *Cibicoides mundulus*, Sr partitioning is strongly buffered by internal pH regulation and ion transport, which maintain a highly supersaturated calcifying fluid despite changes in external seawater chemistry. This implies that Sr/Ca under OAE may not respond directly to external Ω or [CO_3^{2-}], but instead to the extent to which elevated alkalinity alters the chemistry of the internal calcification environment. Additional culture evidence reinforces this species dependence: Sr/Ca correlates with DIC and bicarbonate in shelf *Ammonia* sp. But shows no significant relationship in the deep-sea species *Cassidulina laevigata* (Mojtahid et al., 2023). Sr/Ca should therefore be used cautiously in OAE studies and only with species-specific calibration and, where possible, biomineralization-based interpretation.

Among the additional element-based proxies considered for OAE studies, S/Ca is one of the more mechanistically promising indicators of carbonate chemistry in benthic foraminiferal calcite. Culture experiments show that S/Ca generally increases with increasing pCO_2 and decreasing (CO_3^{2-}) and pH, while remaining relatively insensitive

to salinity, supporting its interpretation as an inverse proxy for carbonate ion concentration when species-specific calibrations are available (Berry, 1998; van Dijk et al., 2017). In cultured *Amphistegina gibbosa* and *Sorites marginalis*, S/Ca rose systematically under more acidified conditions, consistent with greater sulfate incorporation into calcite as carbonate availability declined (van Dijk et al., 2017). Subsequent work indicates that sulfur incorporation is influenced not only by lattice-level SO_4^{2-} substitution for CO_3^{2-} , but also by biomineralization processes, particularly proton-pump activity that modifies pH at the site of calcification (van Dijk et al., 2019). Microscale observations further show that S and Mg are co-located in banded calcite domains associated with organic linings, supporting the view that sulfur incorporation is linked to biologically regulated calcification pathways rather than to external temperature alone (van Dijk et al., 2019). In principle, this suggests that benthic foraminiferal S/Ca could decline under OAE if elevated alkalinity increases (CO_3^{2-}) and saturation state at the site of calcification. However, conflicting responses in other taxa indicate that this proxy is not yet universally transferable, and recent proposals such as the S/Mg ratio should still be regarded as promising proxy for benthic OAE applications (Karancz et al., 2024).

B/Ca provides potentially complementary information on carbonate chemistry, but its behavior is strongly species-dependent and presently less robust than $\delta^{11}\text{B}$ for pH reconstruction. Its application to OAE therefore requires careful calibration and is best interpreted alongside boron isotopes rather than as a stand-alone proxy.

Cd/Ca, Zn/Ca, Mn/Ca, U/Mn, and Al/Ca are best treated as environmental context or screening proxies rather than direct indicators of alkalinity enhancement. Cd/Ca and Zn/Ca primarily reflect nutrient distributions, with some secondary sensitivity to carbonate saturation under more corrosive conditions, but their response above that range appears limited (Marchitto et al., 2000, 2002; Rosenthal et al., 2006). Mn/Ca and U/Mn are more useful for identifying redox overprints and possible authigenic coatings, while Al/Ca serves mainly as a check on residual clay contamination and cleaning efficiency (Boiteau et al., 2012; Rosenthal et al., 2006). Used together, these ratios can help distinguish primary biomineralization signals from changes driven by productivity, redox, diagenesis, or sediment contamination. For OAE studies, their main value is therefore interpretive: they improve confidence that observed changes in primary carbonate-system proxies reflect benthic exposure to alkalinity perturbation rather than secondary environmental or post-depositional effects (Boiteau et al., 2012; Detlef et al., 2020; Rosenthal et al., 2006).

Benthic foraminiferal $\delta^{13}\text{C}$ primarily reflects the isotopic composition of ambient dissolved inorganic carbon (DIC) and is therefore most useful for interpreting bottom-water ventilation, organic-matter remineralization, and microhabitat effects. Epifaunal taxa such as *Cibicidoides wuellerstorfi* commonly record values close to the $\delta^{13}\text{C}$ of bottom-water DIC, whereas infaunal taxa such as *Uvigerina* are typically depleted because they calcify in pore waters enriched in ^{12}C from organic-matter respiration (Hoogakker et al., 2024; Schmittner et al., 2017). Additional species-specific vital effects arise because foraminifera do not calcify in simple inorganic equilibrium but modify carbon speciation at the site of calcification through proton pumping and selective use of dissolved carbon species (Hesse et al., 2014; Toyofuku et al., 2017). CA-mediated inorganic-carbon processing may further modulate this response by accelerating interconversion among dissolved carbon species and facilitating CO_2 supply to calcification (de Goeyse et al., 2021, 2024). In the context of OAE, $\delta^{13}\text{C}$ is therefore unlikely to serve as a direct stand-alone tracer of alkalinity enhancement. Instead, its main value lies in helping to distinguish carbonate-system perturbations from concurrent changes in DIC source, ventilation, or benthic remineralization. Under elevated alkalinity, shifts in DIC speciation may slightly modify benthic foraminiferal $\delta^{13}\text{C}$, but proton-pumping, enzymatic buffering by CA, and preferential CO_2 use are likely to damp or complicate that response rather than produce a simple direct OAE signal (Schmittner et al., 2017; Toyofuku et al., 2017). Used alongside more direct carbonate-system proxies such as $\delta^{11}\text{B}$, U/Ca, or S/Ca, $\delta^{13}\text{C}$ may help separate OAE-related chemical signals from broader environmental variability.

The stable oxygen isotope composition ($\delta^{18}\text{O}$) of benthic foraminiferal calcite primarily reflects bottom-water temperature and the $\delta^{18}\text{O}$ of seawater, which is influenced by hydrography, salinity, and ice-volume effects (Bemis et al., 1998; Shackleton, 1974). For this reason, $\delta^{18}\text{O}$ is not expected to respond directly to alkalinity enhancement in the same mechanistic way as carbonate-system proxies such as $\delta^{11}\text{B}$ or U/Ca. In controlled experiments, it can instead serve as a stability check to confirm that observed geochemical changes are not simply caused by unintended temperature or water-mass variability. In field or sediment-based studies, departures from expected $\delta^{18}\text{O}$ relationships may also help identify diagenetic overprinting or secondary precipitation, particularly when interpreted together with other indicators such as $\delta^{13}\text{C}$, U/Ca, Mn/Ca, or B-based proxies (Marchitto

et al., 2014). Under OAE, $\delta^{18}\text{O}$ should therefore be treated primarily as a contextual and quality-control proxy rather than as a direct recorder of alkalinity addition.

4. Conclusion

Calcareous benthic foraminifera can serve as sensitive indicators of OAE-driven change in benthic environments because their biomineralization is tightly regulated, energy-dependent, and responsive to carbonate-system perturbation. Current evidence suggests that moderate alkalinity increases may reduce the energetic cost of calcification in some taxa, particularly larger benthic foraminifera and under specific exposure settings; However, this should be treated as a species-specific hypothesis rather than a general prediction. The main contribution of this review is to propose an analytical framework that links morphometric, ultrastructural, and geochemical observations to OAE-relevant questions, particularly in deployment settings that directly modify bottom-water or sediment chemistry. A three-tier framework is suggested for the morphological investigations that could be carried out on benthic foraminifera in the framework of OAE research. A four-tier geochemical framework distinguishes primary carbonate-system indicators, pathway-specific tracers, biomineralization-sensitive proxies, and contextual or quality-control indicators. Integrated with concurrent carbonate-system measurements, these frameworks can distinguish biomineralization responses from environmental overprints and establish benthic foraminifera as a standardized biological and mineralogical monitoring component supporting MRV. Future work should therefore prioritize controlled, cross-calibrated direct OAE experiments to define species- and pathway-specific alkalinity thresholds at which benthic foraminiferal calcification is enhanced, remains unchanged, or becomes physiologically constrained.

Conflict of Interest

The authors declare no conflicts of interest relevant to this study.

Availability Statement

No data sets or software were used in this study. Figures were generated using Adobe Photoshop, Adobe Illustrator.

Acknowledgments

The authors declare that no funding was received for this research. George Henry acknowledges the financial support of his PhD scholarship from the University of Milano-Bicocca. We thank the anonymous reviewers which substantially improved the manuscript. We also sincerely thank the Editor-in-Chief, Prof. Robert Kopp, and the Associate Editors for their careful evaluation and valuable guidance throughout the review process. Open access publishing facilitated by Università degli Studi di Milano-Bicocca, as part of the Wiley - CRUI-CARE agreement.

References

- Alves, J. F., Edwards, H. G., Korsakov, A., & De Oliveira, L. F. C. (2023). Revisiting the Raman spectra of carbonate minerals. *Minerals*, 13(11), 1358. <https://doi.org/10.3390/min13111358>
- Bach, L. T., Gill, S. J., Rickaby, R. E., Gore, S., & Renforth, P. (2019). CO₂ removal with enhanced weathering and ocean alkalinity enhancement: Potential risks and co-benefits for marine pelagic ecosystems. *Frontiers in Climate*, 1, 21. <https://doi.org/10.3389/fclim.2019.00007>
- Bach, L. T., Ho, D. T., Boyd, P. W., & Tyka, M. D. (2023). Toward a consensus framework to evaluate air-sea CO₂ equilibration for marine CO₂ removal. *Limnology and Oceanography Letters*, 8(5), 685–691. <https://doi.org/10.1002/lol2.10330>
- Barker, S., Greaves, M., & Elderfield, H. (2003). A study of cleaning procedures used for foraminiferal Mg/Ca paleothermometry. *Geochemistry, Geophysics, Geosystems*, 4(9). <https://doi.org/10.1029/2003GC000559>
- Bassinot, F. C., Mélières, F., Gehlen, M., Levi, C., & Labeyrie, L. (2004). Crystallinity of Foraminifera shells: A proxy to reconstruct past bottom water CO₃²⁻ changes? *Geochemistry, Geophysics, Geosystems*, 5(8). <https://doi.org/10.1029/2003GC000668>
- Bednaršek, N., Van de Mortel, H., Pelletier, G., García-Reyes, M., Feely, R. A., & Dickson, A. G. (2025). Assessment framework to predict sensitivity of marine calcifiers to ocean alkalinity enhancement—Identification of biological thresholds and importance of precautionary principle. *Biogeosciences*, 22(2), 473–498. <https://doi.org/10.5194/bg-22-473-2025>
- Bemis, B. E., Spero, H. J., Bijma, J., & Lea, D. W. (1998). Reevaluation of the oxygen isotopic composition of planktonic foraminifera: Experimental results and revised paleotemperature equations. *Paleoceanography*, 13(2), 150–160. <https://doi.org/10.1029/98PA00070>
- Bentov, S., Brownlee, C., & Erez, J. (2009). The role of seawater endocytosis in the biomineralization process in calcareous Foraminifera. *Proceedings of the National Academy of Sciences of the United States of America*, 106(51), 21500–21504. <https://doi.org/10.1073/pnas.0906636106>
- Berry, J. N. (1998). *Sulfate in foraminiferal calcium carbonate: Investigating a potential proxy for seawater carbonate ion concentration (PhD thesis)*. Massachusetts Institute of Technology.
- Boiteau, R., Greaves, M., & Elderfield, H. (2012). Authigenic uranium in foraminiferal coatings: A proxy for ocean redox chemistry. *Paleoceanography*, 27(3), PA3227. <https://doi.org/10.1029/2012PA002335>
- Borrelli, C., Panieri, G., Dahl, T. M., & Neufeld, K. (2018). Novel biomineralization strategy in calcareous Foraminifera. *Scientific Reports*, 8(1), 10201. <https://doi.org/10.1038/s41598-018-28400-2>
- Brown, R. E., Anderson, L. D., Thomas, E., & Zachos, J. C. (2011). A core-top calibration of B/Ca in the benthic foraminifera *Nuttallides umbonifera* and *Oridorsalis umbonatus*: A proxy for Cenozoic bottom water carbonate saturation. *Earth and Planetary Science Letters*, 310(3–4), 360–368. <https://doi.org/10.1016/j.epsl.2011.08.023>
- Camatti, E., Valsecchi, S., Caserini, S., Barbacci, E., Santinelli, C., Basso, D., & Azzellino, A. (2024). Short-term impact assessment of ocean liming: A copepod exposure test. *Marine Pollution Bulletin*, 198, 115833. <https://doi.org/10.1016/j.marpolbul.2023.115833>

- Carneiro, L. M., dos Santos Rocha, R. S., de Moraes, S. S., Dourado, G. B., Lopes, J. M., Hadlich, G. M., & de Jesus, T. B. (2026). Integrated geochemical and PAH analysis with benthic Foraminifera to assess environmental quality in a tropical estuary. *Environmental Monitoring and Assessment*, 198(8), 843. <https://doi.org/10.1007/s10661-026-15676-5>
- Chen, P., Yu, J., & Jin, Z. (2017). An evaluation of benthic foraminiferal U/Ca and U/Mn proxies for deep ocean carbonate chemistry and redox conditions. *Geochemistry, Geophysics, Geosystems*, 18(2), 617–630. <https://doi.org/10.1002/2016GC006730>
- Clarkson, M. O., Kasemann, S. A., Wood, R. A., Lenton, T. M., Daines, S. J., Richoz, S., et al. (2015). Ocean acidification and the Permo–Triassic mass extinction. *Science*, 348(6231), 229–232. <https://doi.org/10.1126/science.aaa0193>
- Cotton, L. J., Evans, D., & Beavington-Penney, S. J. (2020). The high-magnesium calcite origin of nummulitid Foraminifera and implications for the identification of calcite diagenesis. *PALAIOS*, 35(10), 421–431. <https://doi.org/10.2110/palo.2020.029>
- Cyronak, T., Albright, R., & Bach, L. T. (2023). Field experiments in ocean alkalinity enhancement research. *State of the Planet*, 2, 1–13. <https://doi.org/10.5194/sp-2-oae2023-7-2023>
- Daché, E., Dessandier, P. A., Radhakrishnan, R., Foulon, V., Michel, L., de Vargas, C., et al. (2024). Benthic Foraminifera as bio-indicators of natural and anthropogenic conditions in Roscoff Aber Bay (Brittany, France). *PLoS One*, 19(10), e0309463. <https://doi.org/10.1371/journal.pone.0309463>
- Dale, A. W., Geilert, S., Diercks, I., Fuhr, M., Perner, M., Scholz, F., & Wallmann, K. (2024). Seafloor alkalinity enhancement as a carbon dioxide removal strategy in the Baltic Sea. *Communications Earth & Environment*, 5(1), 452. <https://doi.org/10.1038/s43247-024-01569-3>
- Dämmer, L. K., Ivkić, A., de Nooijer, L., Renema, W., Webb, A. E., & Reichart, G. J. (2023). Impact of dissolved CO₂ on calcification in two large, benthic foraminiferal species. *PLoS One*, 18(8), e0289122. <https://doi.org/10.1371/journal.pone.0289122>
- Dawber, C. F., & Tripathi, A. (2012). Relationships between bottom water carbonate saturation and element/Ca ratios in coretop samples of the benthic Foraminifera *Oridorsalis umbonatus*. *Biogeosciences*, 9(8), 3029–3045. <https://doi.org/10.5194/bg-9-3029-2012>
- DeCarlo, T. M., Comeau, S., Cornwall, C. E., Gajdzik, L., Guagliardo, P., Sadekov, A., et al. (2019). Investigating marine bio-calcification mechanisms in a changing ocean with in vivo and high-resolution ex vivo Raman spectroscopy. *Global Change Biology*, 25(5), 1877–1888. <https://doi.org/10.1111/gcb.14579>
- De Goeyse, S., Lesuis, C., Reichart, G. J., & de Nooijer, L. (2024). The effect of carbonic anhydrase on foraminiferal Mg/Ca. *PeerJ*, 12, e18458. <https://doi.org/10.7717/peerj.18458>
- De Goeyse, S., Raymond, C., Ziveri, P., & Rodolfo-Metalpa, R. (2021). External carbonic anhydrase controls calcification in the large benthic foraminifer *Amphistegina lessona*. *Biogeosciences*, 18, 4305–4323. <https://doi.org/10.5194/bg-18-4305-2021>
- de Nooijer, L. J., Spero, H. J., Erez, J., Bijma, J., & Reichart, G. J. (2014). Biomineralization in perforate Foraminifera. *Earth-Science Reviews*, 135, 48–58. <https://doi.org/10.1016/j.earscirev.2014.03.013>
- de Nooijer, L. J., Toyofuku, T., & Kitazato, H. (2009). Foraminifera promote calcification by elevating their intracellular pH. *Proceedings of the National Academy of Sciences of the United States of America*, 106, 15374–15378. <https://doi.org/10.1073/pnas.0904306106>
- de Nooijer, L. J., Toyofuku, T., Oguri, K., Nomaki, H., & Kitazato, H. (2009). Intracellular pH distribution in Foraminifera determined by the fluorescent probe HPTS. *Biogeosciences*, 6, 2409–2416. <https://doi.org/10.5194/bg-6-2409-2009>
- Detlef, H., Sossian, S. M., Kender, S., Lear, C. H., & Hall, I. R. (2020). Multi-elemental composition of authigenic carbonates in benthic Foraminifera from the eastern Bering Sea continental margin (International Ocean Discovery Program Site U1343). *Geochimica et Cosmochimica Acta*, 268, 1–21. <https://doi.org/10.1016/j.gca.2019.09.025>
- Dettmering, C., Röttger, R., Hohenegger, J., & Schmaljohann, R. (1998). The trimorphic life cycle in foraminifera: Observations from cultures allow new evaluation. *European Journal of Protistology*, 34(4), 363–368. [https://doi.org/10.1016/s0932-4739\(98\)80004-7](https://doi.org/10.1016/s0932-4739(98)80004-7)
- Dias, B. B., Hart, M. B., Smart, C. W., & Hall-Spencer, J. M. (2010). Modern seawater acidification: The response of Foraminifera to high-CO₂ conditions in the Mediterranean Sea. *Journal of the Geological Society*, 167(5), 843–846. <https://doi.org/10.1144/0016-76492010-050>
- Dissard, D., Nehrke, G., Reichart, G. J., & Bijma, J. (2010). Impact of seawater pCO₂ on calcification and Mg/Ca and Sr/Ca ratios in benthic Foraminifera calcite: Results from culturing experiments with *Ammonia tepida*. *Biogeosciences*, 7(1), 81–93. <https://doi.org/10.5194/bg-7-81-2010>
- Dong, S., Lei, Y., Li, T., & Jian, Z. (2020). Response of benthic Foraminifera to pH changes: Community structure and morphological transformation studies from a microcosm experiment. *Marine Micropaleontology*, 156, 101819. <https://doi.org/10.1016/j.marmicro.2019.101819>
- Dubicka, Z., Bojanowski, M. J., Bijma, J., & Bickmeyer, U. (2023). Mg-rich amorphous to Mg-low crystalline CaCO₃ pathway in Foraminifera. *Heliyon*, 9(7), e18331. <https://doi.org/10.1016/j.heliyon.2023.e18331>
- Dubicka, Z., Syczewski, M. D., Benning, L. G., Schreiber, A., Wirth, R., Witkowski, M., et al. (2025). Amorphous calcium carbonate loaded multilamellar vesicles within *Amphistegina* (Rotaliida) Foraminifera. *Acta Biomaterialia*. <https://doi.org/10.1016/j.actbio.2025.02.001>
- Dupont, S., & Metian, M. (2023). General considerations to experimental research on ocean alkalinity enhancement. *State of the Planet Discussions*, 1–11.
- Eisaman, M. D., Geilert, S., Renforth, P., Bastianini, L., Campbell, J., Dale, A. W., et al. (2023). Assessing the technical aspects of ocean-alkalinity-enhancement approaches. *State of the Planet*, 2, 1–29. <https://doi.org/10.5194/sp-2023-1>
- El-Azabi, M., Boukhary, M., Henry, G., & Kassab, W. (2025). New implications for regional biostratigraphy and paleobiogeography of larger benthic Foraminifera in the Lutetian–Bartonian succession of the el-Ramliya–Akheider block, north Eastern Desert, Egypt. *Journal of African Earth Sciences*, 223, 105520. <https://doi.org/10.1016/j.jafrearsci.2024.105520>
- Elderfield, H., Yu, J., Anand, P., Kiefer, T., & Nyland, B. (2006). Calibrations for benthic foraminiferal Mg/Ca paleothermometry and the carbonate ion hypothesis. *Earth and Planetary Science Letters*, 250(3–4), 633–649. <https://doi.org/10.1016/j.epsl.2006.07.041>
- Fantle, M. S., & DePaolo, D. J. (2007). Ca isotopes in carbonate sediment and pore fluid from ODP Site 807A: The Ca²⁺(aq)–calcite equilibrium fractionation factor and calcite recrystallization rates in Pleistocene sediments. *Geochimica et Cosmochimica Acta*, 71(10), 2524–2546. <https://doi.org/10.1016/j.gca.2007.03.006>
- Fantle, M. S., & Higgins, J. (2014). The effects of diagenesis and dolomitization on Ca and Mg isotopes in marine platform carbonates: Implications for the geochemical cycles of Ca and Mg. *Geochimica et Cosmochimica Acta*, 142, 458–481. <https://doi.org/10.1016/j.gca.2014.07.025>
- Fantle, M. S., & Tipper, E. T. (2014). Calcium isotopes in the global biogeochemical Ca cycle: Implications for development of a Ca isotope proxy. *Earth-Science Reviews*, 129, 148–177. <https://doi.org/10.1016/j.earscirev.2013.10.004>
- Faucher, G., Haunost, M., Paul, A., Tietz, A. U. C., & Riebesell, U. (2025). Growth response of *Emiliania huxleyi* to ocean alkalinity enhancement. *Biogeosciences*, 22(2), 405–415. <https://doi.org/10.5194/bg-22-405-2025>
- Faulkner, K. (2023). Phanerozoic evolution trends within benthic Foraminifera. PhD thesis (pp. 1–21). <https://doi.org/10.26153/tsw/45405>
- Fennel, K., Long, M. C., Algar, C., Carter, B., Keller, D., Laurent, A., et al. (2023). Modelling considerations for research on ocean alkalinity enhancement (OAE). *State of the Planet*, 2(oae2023), 9–29. <https://doi.org/10.5194/sp-2-oae2023-9-2023>

- Foster, G. L., & Rae, J. W. (2016). Reconstructing ocean pH with boron isotopes in Foraminifera. *Annual Review of Earth and Planetary Sciences*, 44(1), 207–237. <https://doi.org/10.1146/annurev-earth-060115-012226>
- François, D., Reichart, G. J., & de Nooijer, L. J. (2025). Open or closed: pH modulation and calcification by Foraminifera. *Science Advances*, 11(18), eadq8425. <https://doi.org/10.1126/sciadv.adq8425>
- Fujita, K., Hikami, M., Suzuki, A., Kuroyanagi, A., Sakai, K., Kawahata, H., & Nojiri, Y. (2011). Effects of ocean acidification on calcification of symbiont-bearing reef foraminifera. *Biogeosciences*, 8, 2089–2098. <https://doi.org/10.5194/bg-8-2089-2011>
- Gately, J. A., Kim, S. M., Jin, B., Brzezinski, M. A., & Iglesias-Rodriguez, M. D. (2023). Coccolithophores and diatoms resilient to ocean alkalinity enhancement: A glimpse of hope? *Science Advances*, 9(24), eadg6066. <https://doi.org/10.1126/sciadv.adg6066>
- Girard, E. B., Didaskalou, E. A., Pratama, A. M., Rattner, C., Morard, R., & Renema, W. (2024). Quantitative assessment of reef Foraminifera community from metabarcoding data. *Molecular Ecology Resources*, 24(7), e14000. <https://doi.org/10.1111/1755-0998.14000>
- Glas, M. S., Langer, G., & Keul, N. (2012). Calcification acidifies the microenvironment of a benthic foraminifer (*Ammonia* sp.). *Journal of Experimental Marine Biology and Ecology*, 424, 53–58. <https://doi.org/10.1016/j.jembe.2012.05.006>
- Griffith, E. M., & Fantle, M. S. (2020). *Calcium isotopes* (pp. 1–38). Cambridge University Press.
- Groppelli, S., Calvi, D., Comazzi, F., Jamali Alamooti, S., Azzellino, A., Barbacci, E., et al. (2026). The response of phytoplankton to pH-equilibrated ocean alkalization: A mesocosm experiment with harbour waters. *Marine Pollution Bulletin*, 222, 118787. <https://doi.org/10.1016/j.marpolbul.2025.118787>
- Guamán-Guevara, F., Austin, H., Hicks, N., Streeter, R., & Austin, W. E. N. (2019). Impacts of ocean acidification on intertidal benthic foraminiferal growth and calcification. *PLoS One*, 14(8), e0220046. <https://doi.org/10.1371/journal.pone.0220046>
- Guilhermic, C., Nardelli, M. P., Mouret, A., Le Moigne, D., & Howa, H. (2023). Short-term response of benthic Foraminifera to fine-sediment depositional events simulated in microcosm. *Biogeosciences*, 20(15), 3329–3351. <https://doi.org/10.5194/bg-20-3329-2023>
- Gussone, N., Eisenhauer, A., Rüger, S., Böhm, F., Nægler, T. F., Rehkämper, M., et al. (2003). Model for kinetic effects on calcium isotope fractionation ($\delta^{44}\text{Ca}$) in inorganic aragonite and cultured planktonic Foraminifera. *Geochimica et Cosmochimica Acta*, 67(7), 1375–1382. [https://doi.org/10.1016/s0016-7037\(02\)01296-6](https://doi.org/10.1016/s0016-7037(02)01296-6)
- Gussone, N., & Filipsson, H. L. (2010). Calcium isotope ratios in calcitic tests of benthic foraminifera. *Earth and Planetary Science Letters*, 290(1–2), 108–117. <https://doi.org/10.1016/j.epsl.2009.12.010>
- Gussone, N., & Heuser, A. (2016). Biominerals and biomaterial. In *Calcium stable isotope geochemistry*. Springer Berlin Heidelberg. (pp. 111–144).
- Hall-Spencer, J. M., Rodolfo-Metalpa, R., Martin, S., Ransome, E., Fine, M., Turner, S. M., et al. (2008). Volcanic carbon dioxide vents show ecosystem effects of ocean acidification. *Nature*, 454(7200), 96–99. <https://doi.org/10.1038/nature07051>
- Hallock, P., & Raymond, C. E. (2022). Contributions of trimorphic life cycles to dispersal and evolutionary trends in large benthic foraminifera. *Journal of Earth Science*, 33(6), 1425–1433. <https://doi.org/10.1007/s12583-022-1707-0>
- Hartmann, J., Suitner, N., Lim, C., Schneider, J., Marin-Samper, L., Aristegui, J., et al. (2023). Stability of alkalinity in ocean alkalinity enhancement (OAE) approaches—Consequences for durability of CO_2 storage. *Biogeosciences*, 20(4), 781–802. <https://doi.org/10.5194/bg-20-781-2023>
- Hashim, M. S., Marx, L., Klein, F., Dean, C. L., Burdige, E., Hayden, M., et al. (2025). Mineral formation during shipboard ocean alkalinity enhancement experiments in the North Atlantic. *Biogeosciences*, 22(22), 7149–7165. <https://doi.org/10.5194/bg-22-7149-2025>
- Haynert, K. (2013). *Impact of elevated pCO_2 on benthic Foraminifera from the southwestern Baltic Sea*. (PhD thesis) (pp. 1–202). Christian-Albrechts Universität Kiel.
- Haynert, K., Schönfeld, J., Schiebel, R., Wilson, B., & Thomsen, J. (2014). Response of benthic Foraminifera to ocean acidification in their natural sediment environment: A long-term culturing experiment. *Biogeosciences*, 11(6), 1581–1597. <https://doi.org/10.5194/bg-11-1581-2014>
- Haynes, L., Fehrenbacher, J. S., Baxter, S., Helfand, A., Langston, K., Miller, E., et al. (2025). The impact of ocean alkalinity enhancement on *Globigerinoides ruber* growth and calcification. *AGU Fall Meeting Abstracts*, 2025, OS51D-0432.
- Henry, G., Boukhary, M., & Kassab, W. (2025). Unraveling the Tethyan Eocene: A review of Middle–Upper Eocene *Gaziryna* and allied species in phylogeny, regional biostratigraphy and paleobiogeography. *Acta Geologica Sinica*, 99(6), 1626–1638. <https://doi.org/10.1111/1755-6724.70003>
- Henry, G., El-Azabi, M., & Kassab, W. (2025a). Bartonian coral biostromes in a storm-dominated ramp setting of the El-Ramliya–Akheider block: Sedimentology, sequence stratigraphy and regional paleogeographic insights, Cairo–Sukhna region, Egypt. *Journal of African Earth Sciences*, 224, 105542. <https://doi.org/10.1016/j.jafrearsci.2025.105542>
- Henry, G., El-Azabi, M., & Kassab, W. (2025b). Origin and evolution of Middle Eocene *Nummulites* accumulation in the El-Ramliya–Akheider block, north Eastern Desert, Egypt: New sedimentological insights in a storm-dominated ramp setting. *International Journal of Earth Sciences*, 114(2), 369–390. <https://doi.org/10.1007/s00531-025-02489-z>
- Hermoso, M. (2015). Control of ambient pH on growth and stable isotopes in phytoplanktonic calcifying algae. *Paleoceanography*, 30(8), 1100–1112. <https://doi.org/10.1002/2015PA002844>
- Hesse, T., Wolf-Gladrow, D., Lohmann, G., Bijma, J., Mackensen, A., & Zeebe, R. E. (2014). Modelling $\delta^{13}\text{C}$ in benthic foraminifera: Insights from model sensitivity experiments. *Marine Micropaleontology*, 112, 50–61. <https://doi.org/10.1016/j.marmicro.2014.08.001>
- Ho, D. T., Bopp, L., Palter, J. B., Long, M. C., Boyd, P., Neukermans, G., & Bach, L. (2023). Monitoring, reporting, and verification for ocean alkalinity enhancement. *State of the Planet Discussions*, 1–15. <https://doi.org/10.5194/sp-2023-2>
- Hoogakker, B., Ishimura, T., de Nooijer, L., Rathburn, A., & Schmiedl, G. (2024). A review of benthic foraminiferal oxygen and carbon isotopes. *Quaternary Science Reviews*, 342, 108896. <https://doi.org/10.1016/j.quascirev.2024.108896>
- Iglesias-Rodríguez, M. D., Rickaby, R. E., Singh, A., & Gately, J. A. (2023). Laboratory experiments in ocean alkalinity enhancement research. *State of the Planet Discussions*, 1–19. <https://doi.org/10.5194/sp-2-oae2023-5-2023>
- IPCC: Summary for Policymakers. (2021). In V. Masson-Delmotte, P. Zhai, A. Pirani, S. L. Connors, C. Péan, et al. (Eds.), *Climate change 2021: The physical science Basis. Contribution of Working Group I to the sixth assessment report of the intergovernmental Panel on climate change* (pp. 3–32). Cambridge University Press. <https://doi.org/10.1017/9781009157896.001>
- Jia, Q., Zhang, S., Watkins, J. M., Devriendt, L. S., Huang, Y., & Wang, G. (2024). Modeled foraminiferal calcification and strontium partitioning in benthic Foraminifera helps reconstruct calcifying fluid composition. *Communications Earth & Environment*, 5(1), 35. <https://doi.org/10.1038/s43247-023-01194-6>
- Karancz, S., de Nooijer, L. J., Brummer, G. J. A., Lattaud, J., Haghipour, N., Rosenthal, Y., & Reichart, G. J. (2024). Impact of seawater inorganic carbon chemistry on element incorporation in foraminiferal shell carbonate. *Geochemistry, Geophysics, Geosystems*, 25(4), e2023GC011302. <https://doi.org/10.1029/2023GC011302>
- Keul, N., Langer, G., de Nooijer, L. J., & Bijma, J. (2013). Effect of ocean acidification on the benthic Foraminifera *Ammonia* sp. is caused by a decrease in carbonate ion concentration. *Biogeosciences*, 10, 6185–6198. <https://doi.org/10.5194/bg-10-6185-2013>

- Kim, Y., Caumon, M. C., Barres, O., Sall, A., & Cauzid, J. (2021). Identification and composition of carbonate minerals of the calcite structure by Raman and infrared spectroscopies using portable devices. *Spectrochimica Acta Part A: Molecular and Biomolecular Spectroscopy*, 261, 119980. <https://doi.org/10.1016/j.saa.2021.119980>
- Koukousioura, O., Dimiza, M. D., Triantaphyllou, M. V., & Hallock, P. (2011). Living benthic Foraminifera as an environmental proxy in coastal ecosystems: A case study from the Aegean Sea (Greece, NE Mediterranean). *Journal of Marine Systems*, 88(4), 489–501. <https://doi.org/10.1016/j.jmarsys.2011.06.004>
- Kuroyanagi, A., Irie, T., Kinoshita, S., Kawahata, H., Suzuki, A., Nishi, H., et al. (2021). Decrease in volume and density of foraminiferal shells with progressing ocean acidification. *Scientific Reports*, 11(1), 19988. <https://doi.org/10.1038/s41598-021-99427-1>
- Langer, M. R. (2008). Assessing the contribution of foraminiferan protists to global ocean carbonate production. *Journal of Eukaryotic Microbiology*, 55(3), 163–169. <https://doi.org/10.1111/j.1550-7408.2008.00321.x>
- Lear, C. H., Elderfield, H., & Wilson, P. A. (2000). Cenozoic deep-sea temperatures and global ice volumes from Mg/Ca in benthic foraminiferal calcite. *Science*, 287(5451), 269–272. <https://doi.org/10.1126/science.287.5451.269>
- Lear, C. H., Mawbey, E. M., & Rosenthal, Y. (2010). Cenozoic benthic foraminiferal Mg/Ca and Li/Ca records: Toward unlocking temperatures and saturation states. *Paleoceanography*, 25(4), PA4215. <https://doi.org/10.1029/2009PA001880>
- Lear, C. H., & Rosenthal, Y. (2006). Benthic foraminiferal Li/Ca: Insights into Cenozoic seawater carbonate saturation state. *Geology*, 34(11), 985–988. <https://doi.org/10.1130/G22792A.1>
- Lehmann, N., & Bach, L. T. (2025). Global carbonate chemistry gradients reveal a negative feedback on ocean alkalinity enhancement. *Nature Geoscience*, 18(3), 232–238. <https://doi.org/10.1038/s41561-025-01644-0>
- Levin, L. A., Hönisch, B., & Frieder, C. A. (2015). Geochemical proxies for estimating faunal exposure to ocean acidification. *Oceanography*, 28(2), 62–73. <https://doi.org/10.5670/oceanog.2015.32>
- Marchitto, T. M., Curry, W. B., Lynch-Stieglitz, J., Bryan, S. P., Cobb, K. M., & Lund, D. C. (2014). Improved oxygen isotope temperature calibrations for cosmopolitan benthic Foraminifera. *Geochimica et Cosmochimica Acta*, 130, 1–11. <https://doi.org/10.1016/j.gca.2013.12.034>
- Marchitto, T. M., Curry, W. B., & Oppo, D. W. (2000). Zinc concentrations in benthic Foraminifera reflect seawater chemistry. *Paleoceanography*, 15(3), 299–306. <https://doi.org/10.1029/1999PA000420>
- Marchitto, T. M., Jr., Oppo, D. W., & Curry, W. B. (2002). Paired benthic foraminiferal Cd/Ca and Zn/Ca evidence for a greatly increased presence of Southern Ocean Water in the glacial North Atlantic. *Paleoceanography*, 17(3), 1038. <https://doi.org/10.1029/2000PA000598>
- Mass, T., Giuffrè, A. J., Sun, C. Y., Stiffler, C. A., Frazier, M. J., Neder, M., et al. (2017). Amorphous calcium carbonate particles form coral skeletons. *Proceedings of the National Academy of Sciences of the United States of America*, 114(37), E7670–E7678. <https://doi.org/10.1073/pnas.1707890114>
- Mezger, E. M., de Nooijer, L. J., Boer, W., Brummer, G. J. A., & Reichert, G. J. (2016). Salinity controls on Na incorporation in Red Sea planktonic Foraminifera. *Paleoceanography*, 31(12), 1562–1582. <https://doi.org/10.1002/2016PA003052>
- Mojtahid, M., Depuydt, P., Mouret, A., Le Houdec, S., Fiorini, S., Chollet, S., et al. (2023). Assessing the impact of different carbonate system parameters on benthic Foraminifera from controlled growth experiments. *Chemical Geology*, 623, 121396. <https://doi.org/10.1016/j.chemgeo.2023.121396>
- Moras, C. A., Bach, L. T., Cyronak, T., Joannes-Boyau, R., & Schulz, K. G. (2022). Ocean alkalinity enhancement—avoiding runaway CaCO₃ precipitation during quick and hydrated lime dissolution. *Biogeosciences*, 19(15), 3537–3557. <https://doi.org/10.5194/bg-19-3537-2022>
- Murray, J. W. (2006). *Ecology and applications of benthic Foraminifera* (pp. 1–426). Cambridge university press.
- Nagai, Y., Uematsu, K., Wani, R., & Toyofuku, T. (2018). Reading the fine print: Ultra-microstructures of foraminiferal calcification revealed using focused ion beam microscopy. *Frontiers in Marine Science*, 5, 67. <https://doi.org/10.3389/fmars.2018.00067>
- Nigam, R., & Caron, D. A. (2000). Does temperature affect dimorphic reproduction in benthic foraminifera? A culture experiment on *Rosalina leei*. *Current Science*, 79(8), 1105–1106.
- Nocera, A. C., Traboni, C., Courboulès, J., Romano, F., Chantzas, C., Magiopoulos, I., et al. (2025). The effect of ocean alkalinity enhancement on zooplankton standing stock and community composition in the Eastern Mediterranean Sea: A mesocosm study. *Marine Environmental Research*, 212, 107489. <https://doi.org/10.1016/j.marenvres.2025.107489>
- Oschlies, A., Bach, L., Rickaby, R., Satterfield, T., Webb, R. M., & Gattuso, J. P. (2023). Climate targets, carbon dioxide removal and the potential role of Ocean Alkalinity Enhancement. *State of the Planet Discussions*, 1–11. <https://doi.org/10.5194/sp-2-oae2023-1-2023>
- Pacho, L., de Nooijer, L. J., Boer, W., & Reichert, G. J. (2024). Differences between potassium and sodium incorporation in foraminiferal shell carbonate. *Frontiers in Marine Science*, 11, 1385347. <https://doi.org/10.3389/fmars.2024.1385347>
- Pettit, L. R. (2015). *The effects of ocean acidification on modern benthic Foraminifera* (Doctoral dissertation). University of Plymouth. <https://doi.org/10.24382/4594>
- Prazeres, M., Uthicke, S., & Pandolfi, J. M. (2015). Ocean acidification induces biochemical and morphological changes in large benthic Foraminifera. *Proceedings of the Royal Society B: Biological Sciences*, 282(1803), 20142782. <https://doi.org/10.1098/rspb.2014.2782>
- Rae, J. W. (2018). Boron isotopes in foraminifera: Systematics, biomineralisation, and CO₂ reconstruction. In *Boron isotopes: The fifth element* (pp. 107–143). https://doi.org/10.1007/978-3-319-64666-4_5
- Rae, J. W. B., Foster, G. L., Schmidt, D. N., & Elliott, T. (2011). Boron isotopes and B/Ca in benthic foraminifera: Proxies for seawater carbonate chemistry. *Earth and Planetary Science Letters*, 302(3–4), 403–413. <https://doi.org/10.1016/j.epsl.2010.12.034>
- Raitzsch, M., Kuhnert, H., Hathorne, E. C., Groeneveld, J., & Bickert, T. (2010). Incorporation of Mg and Sr in calcite of cultured benthic foraminifera: Impact of calcium concentration and calcite saturation state. *Biogeosciences*, 7, 869–883. <https://doi.org/10.5194/bg-7-869-2010>
- Raitzsch, M., Kuhnert, H., Hathorne, E. C., Groeneveld, J., & Bickert, T. (2011). U/Ca in benthic foraminifera: A proxy for the deep-sea carbonate saturation. *Geochemistry, Geophysics, Geosystems*, 12(6), Q06018. <https://doi.org/10.1029/2010GC003344>
- Renforth, P., & Henderson, G. (2017). Assessing ocean alkalinity for carbon sequestration. *Reviews of Geophysics*, 55(3), 636–674. <https://doi.org/10.1002/2016RG000533>
- Riebesell, U., Basso, D., Geilert, S., Dale, A. W., Kreuzburg, M., & Meysman, F. (2023). Mesocosm experiments in ocean alkalinity enhancement research. *State of the Planet*, 2-oae2023, 6, 1–33. <https://doi.org/10.5194/sp-2023-11>
- Rosenthal, Y., Lear, C. H., Oppo, D. W., & Linsley, B. K. (2006). Temperature and carbonate ion effects on Mg/Ca and Sr/Ca ratios in benthic foraminifera: Aragonitic species *Hoeglundina elegans*. *Paleoceanography*, 21(1), PA1007. <https://doi.org/10.1029/2005PA001158>
- Russell, A. D., Emerson, S., Nelson, B. K., Erez, J., & Lea, D. W. (1996). Uranium in foraminiferal calcite as a recorder of seawater uranium concentrations. *Geochimica et Cosmochimica Acta*, 60(2), 649–663. [https://doi.org/10.1016/0016-7037\(94\)90497-9](https://doi.org/10.1016/0016-7037(94)90497-9)
- Santinelli, C., Valsecchi, S., Retelletti Brogi, S., Bachi, G., Checcucci, G., Guerrazzi, M., et al. (2024). Ocean liming effects on dissolved organic matter dynamics. *Biogeosciences*, 21(22), 5131–5141. <https://doi.org/10.5194/bg-21-5131-2024>
- Schiebel, R. (2002). Planktic foraminiferal sedimentation and the marine calcite budget. *Global Biogeochemical Cycles*, 16(4), 1065. <https://doi.org/10.1029/2001GB001459>

- Schmittner, A., Bostock, H. C., Cartapanis, O., Curry, W. B., Filipsson, H. L., Galbraith, E. D., et al. (2017). Calibration of the carbon isotope composition ($\delta^{13}\text{C}$) of benthic Foraminifera. *Paleoceanography*, 32(6), 512–530. <https://doi.org/10.1002/2016PA003072>
- Schönfeld, J., Alve, E., Geslin, E., Jorissen, F., Korsun, S., & Spezzaferri, S. (2012). The FOBIMO (FOraminiferal Bio-MONitoring) initiative—Towards a standardised protocol for soft-bottom benthic foraminiferal monitoring studies. *Marine Micropaleontology*, 94, 1–13. <https://doi.org/10.1016/j.marmicro.2012.06.001>
- Schulz, K. G., Bach, L. T., & Dickson, A. G. (2023). Seawater carbonate system considerations for ocean alkalinity enhancement research. *State of the Planet Discussions*, 2023, 1–24. <https://doi.org/10.5194/sp-2023-12>
- Segev, E., & Erez, J. (2006). Effect of Mg/Ca ratio in seawater on shell composition in shallow benthic Foraminifera. *Geochemistry, Geophysics, Geosystems*, 7(2), Q02P09. <https://doi.org/10.1029/2005GC000969>
- Shackleton, N. J. (1974). Attainment of isotopic equilibrium between ocean water and the benthonic Foraminifera genus *Uvigerina*: Isotopic changes in the ocean during the last glacial. In N. R. Anderson & A. Malahoff (Eds.), *The fate of fossil fuel CO₂ in the oceans* (pp. 401–427). Plenum Press.
- Stainbank, S., Spezzaferri, S., Beccari, V., Hallock, P., Adams, A., Angeloz, A., et al. (2020). Photoc stress on coral reefs in the Maldives: The *Amphistegina* bleaching index. *Ecological Indicators*, 113, 106257. <https://doi.org/10.1016/j.ecolind.2020.106257>
- Suitner, N., Faucher, G., Lim, C., Schneider, J., Moras, C. A., Riebesell, U., & Hartmann, J. (2024). Ocean alkalinity enhancement approaches and the predictability of runaway precipitation processes: Results of an experimental study to determine critical alkalinity ranges for safe and sustainable application scenarios. *Biogeosciences*, 21(20), 4587–4604. <https://doi.org/10.5194/bg-21-4587-2024>
- Ter Kuile, B., Erez, J., & Padan, E. (1989). Competition for inorganic carbon between photosynthesis and calcification in the symbiont-bearing foraminifer *Amphistegina lobifera*. *Marine Biology*, 103(2), 253–259. <https://doi.org/10.1007/BF00543355>
- Thibault de Chanvalon, A., Luther, G. W., Estes, E. R., Necker, J., Tebo, B. M., Su, J., & Cai, W. J. (2023). Influence of manganese cycling on alkalinity in the redox stratified water column of Chesapeake Bay. *Biogeosciences*, 20(14), 3053–3071. <https://doi.org/10.5194/bg-20-3053-2023>
- Toyofuku, T., Matsuo, M. Y., de Nooijer, L. J., Nagai, Y., Kawada, Y., Fujita, K., et al. (2017). Proton pumping accompanies calcification in Foraminifera. *Nature Communications*, 8(1), 14145. <https://doi.org/10.1038/ncomms14145>
- Traboni, C., Nocera, A. C., Romano, F., Courboulès, J., Chantzaras, C., Magiopoulos, I., et al. (2025). Plankton do not care: Minimal effects of ocean liming on plankton growth and grazing in the Eastern Mediterranean. *Limnology and Oceanography*, 70(Suppl. 1), S242–S257. <https://doi.org/10.1002/lno.70136>
- van Dijk, I., Barras, C., de Nooijer, L. J., Mouret, A., Geerken, E., Oron, S., & Reichart, G. J. (2019). Coupled calcium and inorganic carbon uptake suggested by magnesium and sulfur incorporation in foraminiferal calcite. *Biogeosciences*, 16(10), 2115–2130. <https://doi.org/10.5194/bg-16-2115-2019>
- van Dijk, I., de Nooijer, L. J., & Reichart, G. J. (2017). Trends in element incorporation in hyaline and porcelaneous Foraminifera as a function of pCO₂. *Biogeosciences*, 14(3), 497–510. <https://doi.org/10.5194/bg-14-497-2017>
- Varliero, S., Alamooti, S. J., Campo, F. P., Cappello, G., Cappello, S., Caserini, S., et al. (2024). Assessing the limit of CO₂ storage in seawater as bicarbonate-enriched solutions. *Molecules*, 29(17), 4069. <https://doi.org/10.3390/molecules29174069>
- Wehrmeister, U., Soldati, A. L., Jacob, D. E., Häger, T., & Hofmeister, W. (2009). Raman spectroscopy of synthetic, geological and biological vaterite: A raman spectroscopic study. *Journal of Raman Spectroscopy*, 40(2), 193–201. <https://doi.org/10.1002/jrs.2438>
- Wit, J. C., de Nooijer, L. J., Wolthers, M., & Reichart, G. J. (2013). A novel salinity proxy based on Na incorporation into foraminiferal calcite. *Biogeosciences*, 10, 6375–6387. <https://doi.org/10.5194/bg-10-6375-2013>
- Zeebe, R. E., & Wolf-Gladrow, D. (2001). *CO₂ in seawater: Equilibrium, kinetics, isotopes Series* (Vol. 65). Gulf Professional Publishing.346.