



1 **Unifying framework for assessing sensitivity of marine calcifiers to ocean alkalinity**
2 **enhancement identifies potential winners, losers and biological thresholds - importance of**
3 **precautionary principle**

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22 Abstract

23 Ocean alkalinity enhancement (OAE), one of the marine carbon dioxide removal strategies, is
24 gaining importance in its role towards alleviating the consequences of climate change as well as
25 mitigating against ocean acidification (OA). OAE is based on adding alkalinity to open-ocean and
26 coastal marine systems through a variety of different approaches, which raises carbonate chemistry
27 parameters (such as pH, total alkalinity, aragonite saturation state), and enhances the uptake of
28 carbon dioxide (CO₂) from the atmosphere. There are large uncertainties in both short- and long-
29 term outcomes related to potential environmental impacts, which would ultimately decide on the
30 success of OAE as a climate strategy. This paper represents a synthesis effort, leveraging on the
31 OA studies, data, observed patterns and generalizable responses. We propose a conceptual
32 framework of categorized responses that are predicted under OAE implementation. The synthesis
33 was done using raw experimental OA data based on 96 collected studies, capturing the responses
34 of eleven biological groups (coralline algae, corals, dinoflagellates, mollusks, gastropods,
35 pteropods, coccolithophores, annelids, crustacean, echinoderms, and foraminifera), using
36 regression analyses to predict biological responses and thresholds to NaOH or Na₂CO₃ additions.
37 Predicted responses were categorized into six different categories (linear positive and negative,
38 threshold positive and negative, parabolic and neutral) to delineate species- and group-specific
39 responders: 40% of species are predicted to respond positively (N=38), 20% of species negatively
40 (N=20), and 40% (N=38) were found to demonstrate a neutral response upon alkalinity addition.
41 For negatively impacted species, biological thresholds corresponding to 10 to 500 μmol/kg NaOH
42 addition were found, occurring at much lower values than previously expected. Such lower
43 threshold values represent realistic conditions related to OAE field deployments but contrast with
44 the conditions where current OAE lab experiments are conducted. We thus explicitly emphasize
45 the importance of including much lower additions of alkalinity in experimental trials to realistically
46 evaluate *in situ* biological responses. Due to practicality and high correlation with Ω_{ar}, we propose
47 using the TA:DIC ratio as a helpful proxy to explore regional applications and biological response
48 to OAE. The ultimate goal of the study is to provide a framework that can serve as a tool for
49 predicting biological responses and thresholds to delineate OAE risks, guide and prioritize future
50 OAE biological research and regional OAE monitoring efforts. With 60% of species showing non-
51 neutral response, a precautionary approach for OAE implementation is warranted, identifying the
52 conditions where potential negative ecological outcomes could happen, which is key for scaling
53 up while also avoiding potential risks.

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59 1. Introduction

60 Anthropogenic carbon dioxide (CO₂) emissions have increased at an unprecedented rate and have
61 contributed to global climate change and negative ecological and biogeochemical impacts in the
62 oceans (Feely et al., 2004; IPCC, 2021; Gattuso et al., 2018), to the extent of crossing six different
63 planetary boundaries (Richardson et al., 2023). Oceans play a crucial role in attenuating the
64 increase in atmospheric CO₂ through the absorption of the excess atmospheric CO₂ of roughly a
65 quarter of anthropogenic carbon dioxide (CO₂) emissions, drawing down around 2–3 Pg C yr⁻¹ in
66 recent decades (Friedlingstein et al., 2022). However, without substantial CO₂ emissions
67 abatement and CO₂ removal strategies, profound repercussions on climate, extreme weather
68 events, and socioeconomic implications will follow. Ocean-based CO₂ removal and sequestration
69 strategies (broadly referred to as marine CDRs) are among the proposed CDR approaches that
70 remove CO₂ and store it for geologically relevant times (National Academies of Sciences,
71 Engineering, and Medicine, 2021). mCDR approaches only complement CO₂ emission reductions
72 and contribute to the portfolio of climate response strategies needed to meet the global goal of
73 limiting warming to well below 2°C as established by the Paris Agreement (UNFCCC, 2015).
74 Various mCDR approaches have unique benefits and costs but differ in their value depending on
75 their state of implementation, and whether they act globally and/or locally (Oschlies et al., 2023).

76 Ocean alkalinity enhancement (OAE) has the potential to mitigate climate change through
77 increasing ocean uptake of CO₂, while simultaneously reversing ocean acidification (OA), and
78 improving marine habitats. Despite being in the concept stage, OAE is viewed with a high level
79 of confidence as to its effectiveness, medium on environmental risk, but low on the underlying
80 knowledge base (Gattuso et al., 2021; National Academies of Sciences, Engineering, and
81 Medicine, 2021). The primary concerns for OAE are large uncertainties in both short- and long-
82 term OAE outcomes related to potential environmental impacts of OAE (Kheshgi, 1995; Bach et
83 al., 2019), especially if OAE were to induce novel conditions in the marine systems that are outside
84 the range of the natural variability, exposing organisms to conditions not experienced in their
85 evolutionary history. The outcome of OAE as a successful climate strategy depends on a thorough
86 and advanced understanding, as yet absent, of the impacts of OAE implementation while avoiding
87 negative biological effects. Unless OAE can be ensured not to show any serious negative impacts
88 on marine organisms, OAE implementation could potentially be halted (Riebesell et al., 2023).

89 1.1 Leveraging ocean acidification research on marine calcifiers

90 Increased CO₂ uptake, which initially is absorbed by the ocean as dissolved CO₂, causes a decline
91 in pH, shoaling of the saturation state horizon (Ω_{ar}) and reduced carbonate ion amount content in
92 a process termed ocean acidification (OA) (Feely et al., 2004), causing negative consequences to
93 marine biota, especially marine calcifiers, the structure and function of the vulnerable marine
94 ecosystem, and alteration of the carbon cycle. On the other hand, chemical changes induced by
95 OAE are inherently linked to reversing the OA process: increasing pH, shifting carbonate
96 chemistry speciation towards lower aqueous carbon dioxide (pCO₂) and higher carbonate ion
97 (CO₂³⁻) amount contents, as well as higher aragonite saturation state (Ω_{ar}). Such changes could
98 either be within the ranges of the variability of the natural systems to which species are



99 acclimatized, or outside them, creating novel conditions for which species might not have
100 developed suitable adaptation strategies. As such, the biological outcomes are, due to their
101 complexity, highly unpredictable.

102 Scientific progress in over 20 years of OA research has brought substantial insights into the
103 biological effects, with the most fundamental outcome being that calcifying organisms would be
104 primarily affected (Riebesell and Gattuso, 2015), with the calcification process being one of the
105 most susceptible pathways, underpinned by species differences in calcification mechanisms (Ries
106 et al., 2009; 2011; Bach et al., 2013; 2015; Leung et al., 2022). However, OA focused heavily on
107 investigating biological effects on the more acidic range of the carbonate chemistry conditions
108 predicted under future scenarios and most of the studies focused on manipulating the level of $p\text{CO}_2$
109 rather than alkalinity. This resulted in poor understanding of the biological effects at the alkaline
110 end of the carbon chemistry range (Renforth and Henderson, 2017). Some biological inferences
111 can be made based on the understanding of the physiological mechanisms underlying the
112 calcification mechanisms (Bach et al., 2019), but such insights do not provide sufficient
113 understanding.

114 Despite the lack of biological data at the upper ranges of pH and Ω_{ar} , this study builds on the
115 premise that previous OA studies could be leveraged to establish a framework of biological
116 responses under OAE. Despite more nuanced species-specific responses, there are patterns of OA
117 sensitivity that hold across the pathways as well as the functional groups (Ries et al., 2009; 2011).
118 In addition, comparative experimental work, meta-analyses, and the threshold work (Kroeker et
119 al., 2013; Leung et al., 2022; Bednaršek et al., 2019, 2020, 2021) have indicated that even very
120 diverse responses can be grouped into categorical responses. This study aims at establishing a
121 systematic framework for categorizing responses under OAE impact, specifically looking at the
122 calcification rate responses.

123 **1.2 Testable conceptual framework based on the existing OA studies**

124 Based on Ries et al. (2009), calcification responses can be categorized into six categories (Fig. 1):
125 linear positive or negative response; threshold positive or negative response (exponential fit);
126 parabolic response; and neutral (no significant) response. We hypothesize that similar categories
127 of responses, as delineated by Ries et al. (2009, 2011), could also be applicable to the OAE dosing.
128 For this meta-analyses, we have undertaken three steps: first, synthesize carbonate chemistry data
129 at regional and global scales to obtain TA, DIC and Ω_{ar} correlations; second, conduct a literature
130 review and collect available data from OA literature related to the calcification rate responses
131 across the species of eleven groups of marine calcifiers; and third, run regression analyses and
132 determine the category of calcification rate response to TA:DIC, further extending it with addition
133 of NaOH and Na_2CO_3 . We propose to operate with the TA:DIC ratio because the TA:DIC ratio
134 essentially controls the value of Ω_{ar} (Bach et al., 2019) even though alkalinity itself does not
135 directly affect biological responses. Here, we demonstrate its relationship with biological
136 outcomes and show the application for the TA:DIC thresholds beyond which the responses become
137 negative. Ultimately, we synthesize which calcifying species or groups are predicted to benefit or
138 lose to OAE, what constitutes a species-specific safe operating space related to the OAE and



139 delineate what experiments are most urgently needed before massive OAE field implementation
140 occurs.

141

142 **2. Methodology**

143 **2.1 Extraction of the carbonate chemistry data from the GLODAP dataset**

144 We extracted total alkalinity, dissolved inorganic carbon, Ω_{ar} , and pH from the Global Ocean Data
145 Analysis Project GLODAPv2.2023 dataset (<https://glodap.info>). We used regression in MATLAB
146 with a second-order polynomial equation to predict Ω_{ar} from the TA:DIC. The regression analysis
147 was performed using data from various depth intervals (0–10m, 0–30m, 0–50m, 0–100m, 0–200m)
148 regionally and globally. The regional analysis divided the global oceans into the following
149 groupings: Arctic (north of 65°N), Southern (south of 40°S), North Pacific (north of 40°N), Central
150 Pacific (40°S to 40°N), North Atlantic (North of 40°N), Central Atlantic (40°S to 40°N), and
151 Indian Ocean (north of 40°S).

152 **2.2 Literature review of ocean acidification data collection**

153 To assess the impact of OAE on a range of marine calcifiers, we used existing studies on marine
154 species calcification response that had aligned raw biological (calcification rate) data along with
155 the carbonate chemistry. We searched within Scopus, Web of Science, and PubMed and then used
156 the datasets that were archived in NCEI, OA-ICC and Pangea. Through personal correspondence,
157 we have additionally contacted lead authors of the studies, whose data are not or are insufficiently
158 archived, mostly to validate the predicted response. If we received data through this way, that was
159 explicitly acknowledged in the dataset. These searches for the biological datasets related to
160 calcification and corresponding carbonate chemistry were carried out until November 2023 and
161 cover 96 existing studies, with the aim to cover a wide range of calcifying organisms across various
162 functional groups and 82 species. This data was compiled, and units standardized where possible.
163 The functional groups and categories of response were based on the typology of OA response as
164 described by Ries et al. (2009) and Ries (2011).

165 The main issue when compiling data was the lack of standardization of the calcification rates. A
166 variety of calcification rate units were used across different studies. Where possible, the units were
167 converted to mmol of CaCO_3 g weight⁻¹ hr⁻¹. However, the data required to do so was not always
168 readily available. Other units used for calcification rate were mmol of CaCO_3 m⁻² h⁻¹ and mmol of
169 CaCO_3 m⁻³ hr⁻¹, and there was also data used as an indication of calcification rate with units mmol/#
170 h⁻¹, mmol h⁻¹, mmol/# h⁻¹, mmol cm⁻², % h⁻¹, where ‘#’ indicates one individual. Growth rates were
171 used as indicators of calcification rate for single-cell organisms. Data were analyzed on a species
172 level. Where there were multiple studies available for the calcification rate of one species using
173 the same rate units, the data were combined (see example for the coccolithophores). The final
174 response for those species was chosen by the study with the most data points and lowest p-value.

175 **2.3 Sorting species-specific responses into categories per calcification response**

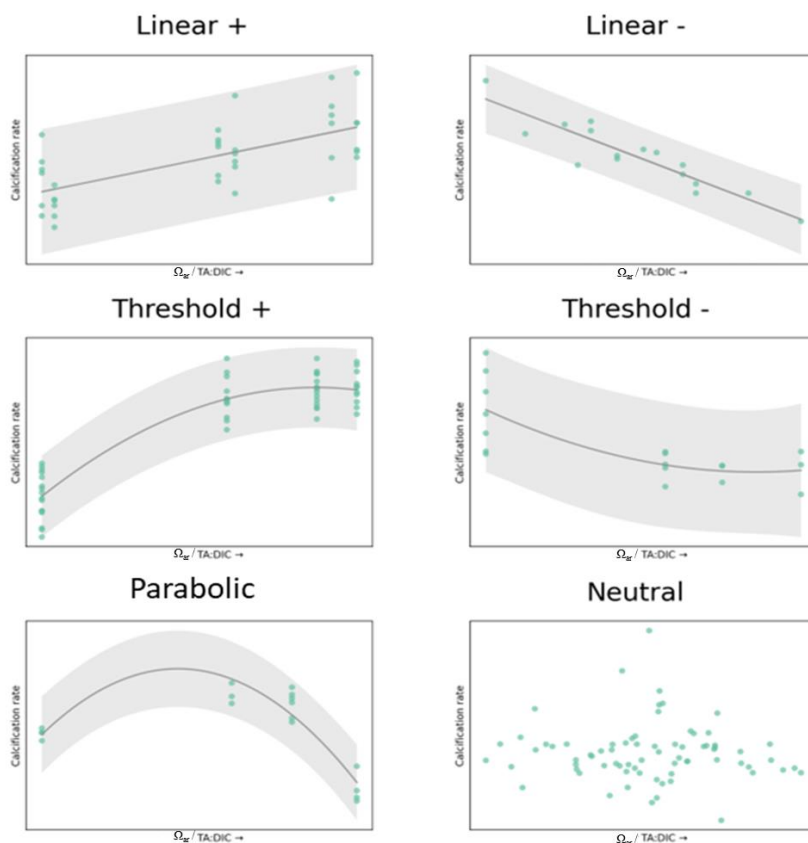


176 As mentioned above, the categories of calcification rate responses were replicated based on Ries
177 et al., (2009) the species' responses to Ω_{ar} were split into 6 categories (Fig. 1): linear positive and
178 linear negative, parabolic, threshold positive and negative, and neutral, whatever was the best as
179 determined by their respective regression models (using the ordinary least squares method in
180 Statsmodels for Python, see Seabold et al. (2010)). The regression with the lowest mean squared
181 error and highest goodness of fit (R^2) value was chosen as having the best fit. Where a linear
182 regression having the best fit, we assigned a linear response, which could be either positive or
183 negative based on the slope. The species with a significant exponential fit were categorized as
184 threshold positive (+) or threshold negative (-) (Ries et al., 2009), which was distinguished from
185 the parabolic response with the fitted parabolic curve.

186 The best fit regression was assigned to each species and plotted, but only if the p-value was
187 considered significant, i.e. lower than 0.1. These regressions were plotted along with a 90%
188 prediction interval, which accounts for the variability of the experimental data. The species with a
189 p-value > 0.1 were categorized as having no correlation. The decision for greater than 0.05 p value
190 was made because a lot of studies showed a strong trend in a response but were not significant at
191 $p < 0.05$.

192 A more practical way of looking at the impacts of the OAE treatment is by using the changes in
193 the TA:DIC ratio instead of using a single carbonate parameter because of the highly correlative
194 relationship between them (Fig. 3). As such, regression models were also applied to TA:DIC vs
195 calcification rate. Their best fit regressions and responses were the same as for Ω_{ar} vs calcification
196 rate. See Fig. 1 for an overview of the responses of calcification rate to increasing Ω_{ar} and TA:DIC.
197 For each regression, the Root Mean Square Error (RMSE) was computed.

198 The TA:DIC threshold was computed to indicate the point at which calcification rate is reduced
199 by a half (linear negative and threshold negative), or as a point at which the calcification rate is
200 predicted to change slope (see Supplementary Fig. 2, Tables 2, 3). Once the species' responses
201 were determined, an attempt was made to group them based on functional groups. However, the
202 wide range of species' responses per group meant the spread of data was often too large to see any
203 meaningful overall response. Therefore, most of the analysis remained on the species level (Table
204 1).



205

206 **Figure 1:** Overview of the categories of responses between carbonate chemistry parameters (Ω_{ar}
 207 /TA:DIC) and calcification rate: linear positive (calcification increase at higher Ω_{ar} /TA:DIC),
 208 linear negative (calcification decrease at higher Ω_{ar} /TA:DIC), exponential for the threshold
 209 positive response (calcification increase with plateauing at higher Ω_{ar} /TA:DIC), exponential for
 210 the threshold negative response (calcification decline with plateauing at lower Ω_{ar}) and parabolic
 211 (calcification increase followed by a decrease at higher Ω_{ar} /TA:DIC). Responses were only
 212 considered significant when $p < 0.1$, otherwise they were categorized as neutral.

213 2.4 Conceptual framework to evaluate increases in TA:DIC

214 The regression models applied to each species could be used to predict calcification rates at higher
 215 TA:DIC ratio. We added alkalinity at the average of the response form OA dataset, and this was
 216 computed for each functional group, representing a baseline for NaOH additions. From this
 217 baseline, TA was added in the form of both NaOH and Na₂CO₃. These two compounds were
 218 chosen as they differentially change the carbonate chemistry settings, with NaOH changing
 219 TA:DIC in the 1:1 ratio, while Na₂CO₃ inducing 2:1 TA:DIC change. For example, 10 μmol/kg of
 220 NaOH addition will increase TA by 10 μmol/kg and not affect DIC. For Na₂CO₃, 10 μmol/kg



221 addition will increase TA by 10 $\mu\text{mol/kg}$ and increase DIC by 5 $\mu\text{mol/kg}$. The Deffeyes diagrams
222 presented in Schulz et al. (2023) demonstrated the usefulness of this approach. For both NaOH
223 and Na_2CO_3 , 10 $\mu\text{mol/kg}$ was conceptually added, and the carbonate system was recomputed. This
224 was repeated for increments of 100 $\mu\text{mol/kg}$ up until a total of 500 $\mu\text{mol/kg}$. The new TA:DIC
225 ratios were estimated using the ratio of the new TA and DIC by adding the direct effect of ΔTA
226 and ΔDIC due to chemical additions of NaOH (assume $\Delta\text{DIC}=0$) or Na_2CO_3 (assume
227 $\Delta\text{DIC}=0.5*\Delta\text{TA}$). A maximum of 500 $\mu\text{mol/kg}$ was chosen to have more realistic additions of TA
228 that resemble those appropriate within the OAE field trials (e.g. Wang et al., 2023).

229 With the new TA:DIC ratios after TA addition, the species' regression models based on the fitted
230 OA response data were used to compute respective calcification rates (note that added points with
231 NaOH or Na_2CO_3 were not calculated as part of the regression). These data points were all plotted
232 along with the experimental data, regression model and prediction intervals as shown in Fig. 2.
233 The TA:DIC values at which the prediction interval exceeds four standard deviation were also
234 calculated to indicate the limit of what TA:DIC we can accurately predict calcification rates.

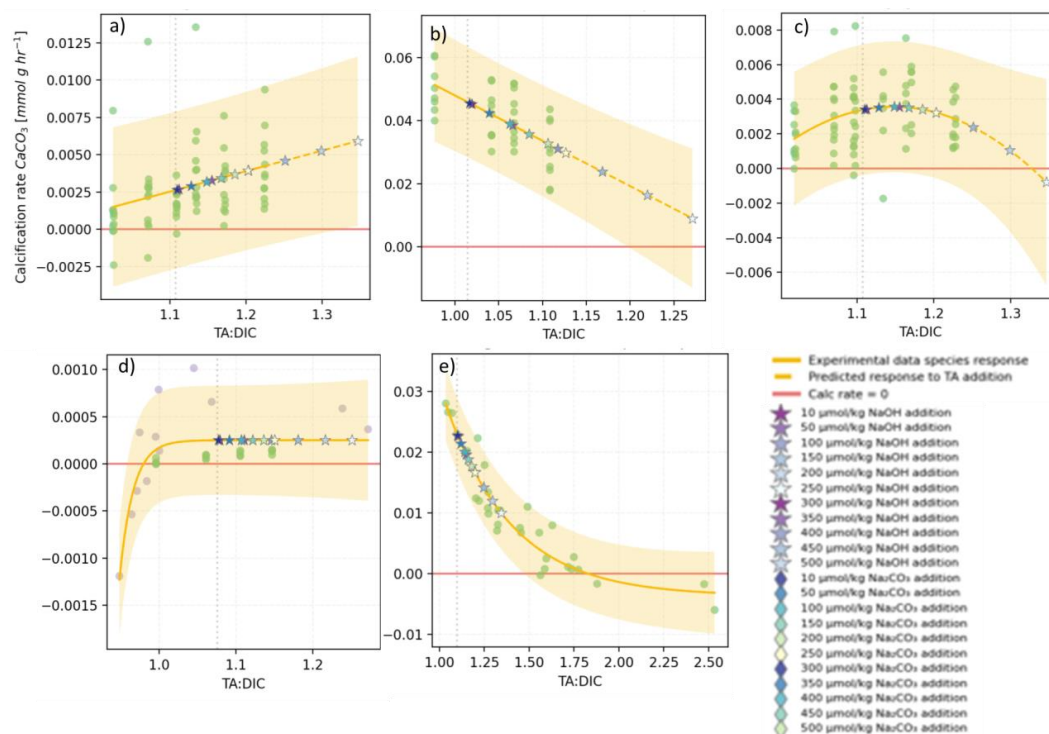
235 **2.5 Evaluation of the biological responses based on the OAE addition**

236 The species with significant correlations were grouped visually based on their best-fit regression
237 models and are classified into positive, negative, and neutral as the following:

238 1) *Positive responders*: species with predicted linear positive and threshold positive calcification
239 rate response corresponding with increased TA addition.

240 2) *Negative responders*: species with predicted *linear negative, parabolic and threshold negative*
241 *response* in calcification rate upon TA addition. For the parabolic and threshold negative response,
242 a concentration of NaOH was determined that indicates the threshold in TA:DIC ratio beyond
243 which the response becomes negative. Additionally, NaOH concentration was determined to
244 reduce the calcification rate to a half, with the threshold at the corresponding TA:DIC.

245 3) *Neutral responders*: species with *no significant correlation* ($p < 0.05$) in calcification rate upon
246 TA addition.



247

248 **Figure 2:** Conceptual diagram to show how experimental data, predicted values at various
 249 additions of alkalinity, the regression line and prediction error margins are fitted for a) linear
 250 positive; b) linear negative; c) parabolic; d) exponential for with threshold positive; e) exponential
 251 for negative with threshold negative. The uncertainty interval indicates four standard deviations.
 252 Blue horizontal dotted line indicates reduction of calcification rate to half of its values, and the
 253 red line indicates zero net dissolution (calcification rate is equal to 0; dissolution rate =
 254 calcification rate).

255 **3. Results**

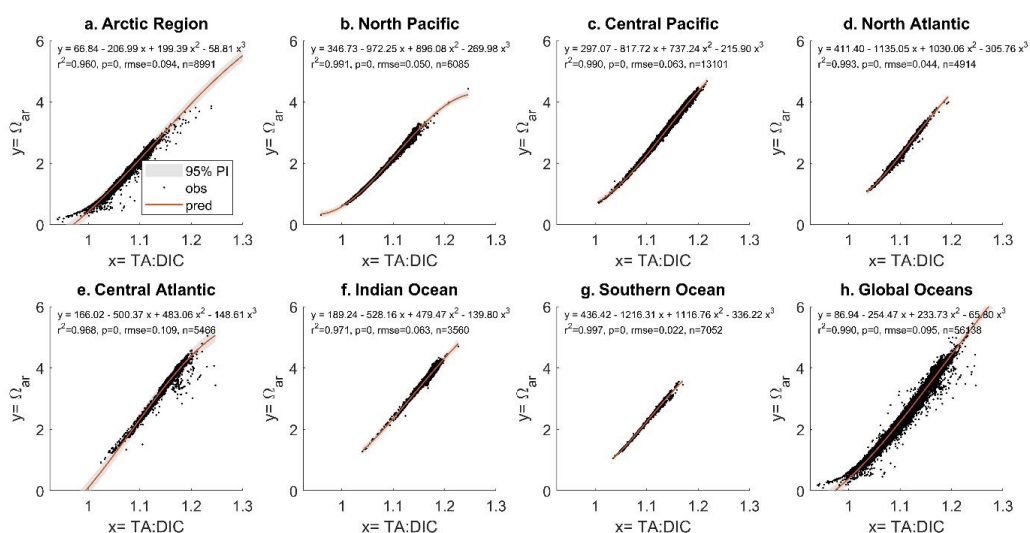
256 **3.1 Global and regional carbonate chemistry data coverage**

257 The compilation of chemical observational data (pH, Ω_{ar} , TA, DIC) was done for the GLODAP
 258 data across the regional ocean and global scales to determine the range of Ω_{ar} , TA and DIC (as
 259 represented by the TA:DIC ratio) and TA:DIC vs Ω_{ar} correlation down to the depths averaged over
 260 200 m. Here, we focus on showing the results ranging over the 0–50m because this covers most of
 261 the biological habitat for examined species and it is where the OAE enhancement would induce
 262 the greatest changes. Over the 0–50 m depth, Ω_{ar} ranges from 0.2 to 5 and TA:DIC ranges from
 263 0.1 to 1.25 and both parameters are correlated across all the regions, as demonstrated by the fitted
 264 second-order polynomial regressions, with R^2 of 0.96 or higher, and all the correlations being
 265 significant (Fig. 3), with regional specific relationships not impacting the fit. All the correlation



266 parameters are presented in Supplementary Table 1. Similar fits were found at different depths.
 267 The conditions in the higher latitude regions are located at the lower range of Ω_{ar} vs TA:DIC, while
 268 the conditions in the low latitudes and temperate regions are at the upper range, with the highest
 269 values present in the central Atlantic and Pacific region.

270 Such strong correlation as observed for Ω_{ar} vs TA:DIC does not exist with pH, regardless of the
 271 depth interval examined. While the correlations are still significant, they are broadly distributed
 272 and represented over a shorter TA:DIC range, with significantly lower goodness of fit
 273 (Supplementary Fig. 1), with the correlations being highly regionally dependent due to pH and
 274 temperature co-linearity. Because of this, all further biological analyses are only done using the
 275 Ω_{ar} vs TA:DIC ratio.



276

277 **Figure 3:** The range of observed Ω_{ar} and DIC and TA values (as represented by the TA:DIC ratio)
 278 values and the relationship with the best fitted curve between Ω_{ar} vs TA:DIC across regional (a-g)
 279 and global (h) scales based on the observational GLODAP dataset averaged over 0-50 m depth.

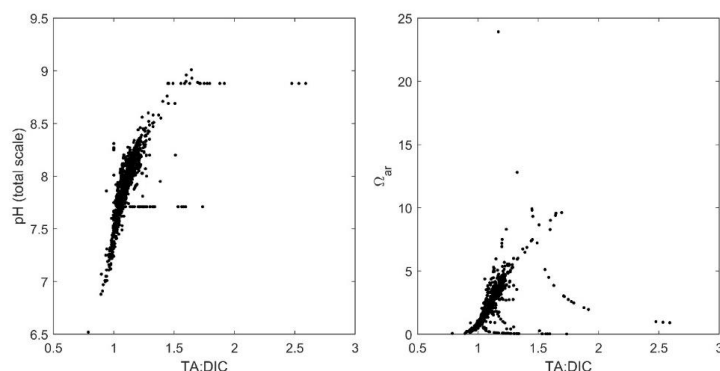
280 3.2 Biological experimental data from the OA studies

281 Biological data from the OA experimental studies was compiled to determine the range of Ω_{ar}
 282 experimental conditions used and their TA:DIC relationship (Fig. 4). Most studies covered pH
 283 conditions up to 8.5 and Ω_{ar} up to 5, with a few studies increasing pH up to 8.8 and Ω_{ar} of 15. This
 284 indicates the potential of leveraging such experimental studies as a baseline for predictive
 285 regression models of biological responses to a range of Ω_{ar} conditions, as expected under OAE
 286 studies. We also observed that experimental data ranges were not always consistent with natural
 287 conditions, for example, having a lower Ω_{ar} at a higher TA:DIC ratio.

288 In addition, plotting biological data from the OA datasets against the regional and global TA:DIC
 289 gradient (Fig. 8), it is obvious that various biological groups are clustered around specific TA:DIC



290 ratios, for example, mollusks and corals are represented on the lower and higher TA:DIC gradients,
291 respectively, while dinoflagellates are randomly scattered off the TA:DIC line. This indicates that
292 there is a general lack of data distribution in the upper ranges of TA:DIC ratio, especially for the
293 groups that are lying at the lower and mid end of the TA:DIC ratio spectra.

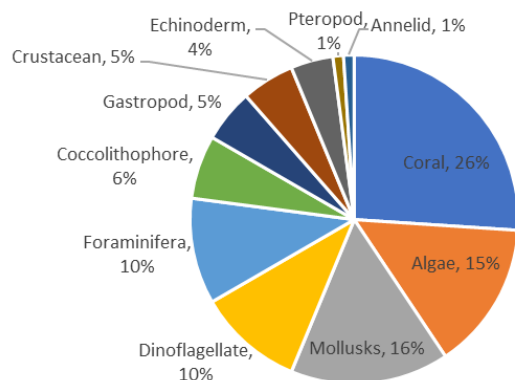


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295 **Figure 4:** Chemical data for TA:DIC vs Ω_{ar} used in the experimental OA treatments.

296 3.3 Data collection for the calcification rate responses of different biological groups

297 We examined 96 datasets, which covered 82 different species that were divided into 9 different
298 groups (Fig. 5). These functional groups were corals (26% of datasets), calcifying algae (15%),
299 mollusks (16%), foraminifera (10%), dinoflagellates (10%), coccolithophores (6%), gastropods
300 (5%), crustaceans (5%), echinoderms (4%), pteropods (1%), and annelids (1%). In the mollusks
301 group, we have separated out the gastropod and pteropod because there of a higher number of
302 studies that explicitly cover for these two groups. The group of gastropods refers to all gastropods
303 that are not pteropods. If all three groups were combined (mollusks, gastropods, pteropods), this
304 group would be the second most representative.



305

306



307 **Figure 5:** *Percent of studies for multiple groups (N=11) with available data for the calcification*
308 *rate responses as part of data compilation of 98 studies).*

309

310 **3.4 Species-specific responses to NaOH/Na₂CO₃ addition**

311 Calcification rate responses of species from different groups were correlated to Ω_{ar} vs TA:DIC
312 and summarized to obtain calcification rate response (Figs. 1, 2; Table 1). The calcification rate
313 responses encompassed linear (positive and negative), exponential (positive and negative),
314 parabolic, and neutral responses, with the slope and the intercept of the response determining the
315 type and the magnitude of the response. We present fitted responses of calcification rate per
316 TA:DIC ratio for each examined species (Table 1, Supplementary Fig. 2). When possible, we fitted
317 a regression to multiple datasets of the same species that used the same units. We also present the
318 response with the additions of NaOH and Na₂CO₃ on a species level (Supplementary Fig. 2) and
319 their biological TA:DIC thresholds (Table 2). The uncertainty of the responses was evaluated as
320 the prediction interval where four standard deviation intervals are exceeded, which indicated the
321 maximum ratio that allows for accurate prediction of the calcification rate.

322 Within each of the 11 groups, several categories of calcification response occur within each
323 functional group, with the most varied being the group of coralline algae, dinoflagellates,
324 foramenifera and mollusks, with each of them showing 4 or 5 different categories of calcification
325 responses (Fig. 6). Of the six types of responses of calcification rate vs TA:DIC, 28% were linear
326 positive (N=27), 10% linear negative (N=10), 12% threshold positive (N=11), 3% threshold
327 negative (N=3), 7% parabolic (N=10) and 40% neutral (N=38).

328 **Table 1:** *This table includes all the studies OA data was collected, the name of the species and*
329 *group it belongs to, and the accompanying calcification rate unit. The most significant regressions*
330 *(with at least $p < 0.1$) per species and rate unit are shown, the p-value, goodness of fit (R^2) and*
331 *Root Mean Square Error (RMSE). The type of regression (linear positive or negative, threshold*
332 *positive or negative, parabolic, and neutral (not significant) as well as an overall response*
333 *(positive, negative, neutral) is indicated.*

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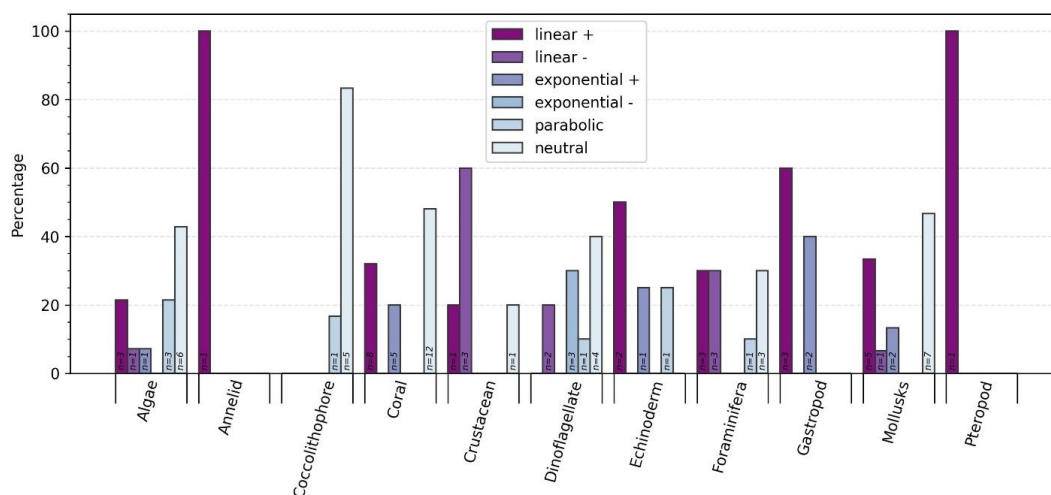
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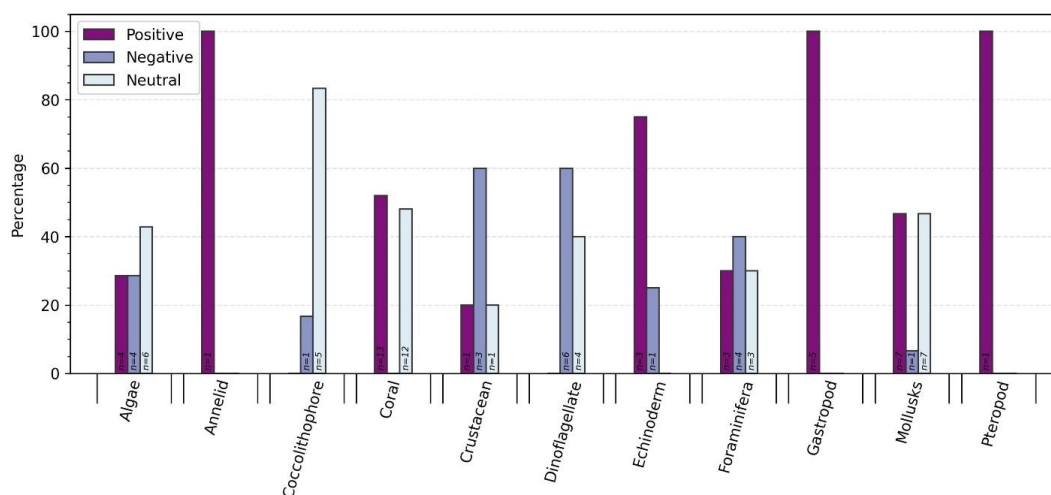
Studies	# Datapoints	Group	Species	Rate unit	Response	Type of response	p-value	R2	rmse
Camp et al. (2017)	2	Coral	<i>Acropora formosa</i>	[mmol/m-2/hr]	neutral	Neutral			
Meyer et al. (2016)	24	Coral	<i>Acropora millepora</i>	[mmol/m-2/hr]	neutral	Neutral			
Camp et al. (2017), Comeau et al. (2013)	74	Coral	<i>Acropora pulchra</i>	[mmol/m-2/hr]	exponential +	Positive	0	0.29	1.330E+03
Agostini et al. (2021)		Coral	<i>Acropora solitaryensis</i>	[mmol/m-2/hr]	neutral	Neutral			
Comeau et al. (2013), Comeau et al. (2019)	81	Coral	<i>Acropora yongei</i>	[mmol/m-2/hr]	linear +	Positive	0	0.29	1.945E+04
Tatters et al. (2013)	45	Dinoflagellate	<i>Alexandrium sp.</i>	[1/hr]	neutral	Neutral			
Keut et al. (2013)	205	Foraminifera	<i>Ammonia sp.</i>	[mmol/m-3/hr]	linear -	Negative	0.028	0.02	2.16E+10
Pansch et al. (2014)	36	Crustacean	<i>Amphibalanus</i>	[mmol/g/hr]	linear +	Positive	0	0.43	4.444E-04
Vasquez-Elizondo et al. (2015)	4	Algae	<i>Amphiroa tribulus</i>	[mmol/m*2/hr]	neutral	Neutral			
Prazeres et al. (2015)	32	Foraminifera	<i>Amphistegina lessonii</i>	[%/hr]	parabolic	Negative	0.001	0.39	1.038E-03
Ries et al. (2009)	17	Echinoderm	<i>Arbacia punctulata</i>	[mmol/g/hr]	parabolic	Negative	0	0.89	3.114E-04
Ries et al. (2009)	18	Mollusks	<i>Argopecten irradians</i>	[mmol/g/hr]	linear +	Positive	0.01	0.35	1.692E-04
Ramajo et al. (2016)	6	Mollusks	<i>Argopecten purpuratus</i>	[mmol/g/hr]	linear -	Negative	0.075	0.59	1.22E+10
Zhang et al. (2011)	5	Mollusks	<i>Azumpecten farreri</i>	[mmol/g/hr]	linear +	Positive	0.011	0.92	6.81E+10
Florini et al. (2011), Langer et al. (2011)	8	Coccolithophore	<i>Calcidiscus leptoporus</i>	[mmol/#/hr]	neutral	Neutral			
Langer et al. (2006)	6	Coccolithophore	<i>Calcidiscus leptoporus</i>	[mmol/m-3/hr]	neutral	Neutral			
Ries et al. (2009)	36	Crustacean	<i>Callinectes sapidus</i>	[mmol/g/hr]	linear -	Negative	0	0.4	8.195E-03
Hansen et al. (2007)	19	Dinoflagellate	<i>Caratium lineatum</i>	[#/hr]	exponential -	Negative	0	0.69	4.156E-03
Ong et al. (2017)	24	Mollusks	<i>Cerastoderma edule</i>	[mmol/g/hr]	neutral	Neutral			
Sordo et al. (2021)	27	Mollusks	<i>Chamaelea gallina</i>	[mmol/g/hr]	neutral	Neutral			
Langer et al. (2006)	3	Coccolithophore	<i>Coccolithus pelagicus</i>	[mmol/h]	neutral	Neutral			
Camp et al. (2017)	2	Coral	<i>Coelastrea aspera</i>	[mmol/m-2/hr]	neutral	Neutral			
Manriquez et al. (2016)	74	Gastropod	<i>Concholepas</i>	[mmol/g/hr]	linear +	Positive	0	0.24	9.395E-04
Gazeau et al. (2007)	20	Mollusks	<i>Crossostrea gigas</i>	[mmol/g/hr]	linear +	Positive	0	0.61	3.79E+10
Ries et al. (2009), Waldbusser et al. (2011)	28	Mollusks	<i>Crossostrea virginica</i>	[mmol/g/hr]	exponential +	Positive	0	0.56	2.611E-04
Noblet et al. (2016), Ries et al. (2009)	173	Gastropod	<i>Crepidula fornicata</i>	[mmol/g/hr]	exponential +	Positive	0	0.19	2.799E-03
Garilli et al. (2015)		Mollusks	<i>Cyclope neritea</i>	[mmol/g/hr]	neutral	Neutral			
Bove et al. (2020)	27	Coral	<i>Duncanopsammia</i>	[mmol/m-2/hr]	linear +	Positive	0.002	0.33	5.075E+04
Courtney et al. (2015)	28	Echinoderm	<i>Echinometra viridis</i>	[%/h]	linear +	Positive	0.001	0.35	1.304E+04
Courtney et al. (2021)	4	Echinoderm	<i>Echinometra viridis</i>	[1/hr]	linear +	Positive	0.024	0.95	2.385E+03
	111	Coccolithophore	<i>Emiliania huxleyi</i>	[mmol/m-3/hr]	parabolic	Negative	0.013	0.09	6.460E+03
Ries et al. (2009)	18	Echinoderm	<i>Eucidaris tribuloides</i>	[mmol/g/hr]	exponential +	Positive	0	0.84	3.592E-04
Kisakurek et al. (2011)	16	Foraminifera	<i>Globigerinella</i>	[mmol/hr]	neutral	Neutral			
Kisakurek et al. (2011)	14	Foraminifera	<i>Globigerinoides ruber</i>	[mmol/hr]	neutral	Neutral			
Cornwall et al. (2018)	44	Coral	<i>Goniopora sp.</i>	[mmol/m-2/hr]	neutral	Neutral			
Tatters et al. (2013)	45	Dinoflagellate	<i>Gonyaulax sp.</i>	[1/hr]	neutral	Neutral			
Sinutok et al. (2011)	16	Algae	<i>Halimeda cyindracea</i>	[mmol/hr]	neutral	Neutral			
Meyer et al. (2016)	71	Algae	<i>Halimeda macroloba</i>	[mmol/m-2/hr]	linear -	Negative	0.616	0.01	9.476E-03
Comeau et al. (2013)	24	Algae	<i>Halimeda macroloba</i>	[mmol/g/hr]	parabolic	Negative	0.013	0.12	2.774E-03
Sinutok et al. (2011)	16	Algae	<i>Halimeda macroloba</i>	[mmol/g/hr]	parabolic	Negative	0.011	0.5	1.447E-04
Comeau et al. (2013)	62	Coral	<i>Halimeda minima</i>	[mmol/g/hr]	neutral	Neutral			
Meyer et al. (2016)	24	Algae	<i>Halimeda opuntia</i>	[mmol/m-2/hr]	linear +	Positive	0.008	0.28	2.218E-02
Hansen et al. (2007)	31	Dinoflagellate	<i>Heterocapsa triquetra</i>	[#/hr]	exponential -	Negative	0	0.91	2.722E-03
Ries et al. (2009)	18	Crustacean	<i>Homarus americanus</i>	[mmol/g/hr]	linear -	Negative	0.001	0.48	7.901E-03
Ries et al. (2009)	41	Annelid	<i>Hydroides crucigera</i>	[mmol/g/hr]	linear +	Positive	0.073	0.08	2.669E-04
Comeau et al. (2013)	72	Coral	<i>Hydroolithon reinboldii</i>	[mmol/g/hr]	linear +	Positive	0.005	0.11	2.586E-03
Cornwall et al. (2018)	23	Coral	<i>Hydroolithon reinboldii</i>	[mmol/m-2/hr]	neutral	Neutral			
Wang et al. (2019)	4	Dinoflagellate	<i>Karenia mikimotoi</i>	[#/hr]	linear -	Negative	0.063	0.88	4.947E-04
Comeau et al. (2009), Comeau et al. (2010)	12	Pteropod	<i>Limacina helicina</i>	[mmol/g/hr]	linear +	Positive	0	0.85	8.430E+10
Tatters et al. (2013)	45	Dinoflagellate	<i>Lingulodinium</i>	[1/hr]	neutral	Neutral			
Comeau et al. (2013)	72	Coral	<i>Lithophyllum faveescens</i>	[mmol/g/hr]	exponential +	Positive	0.068	0.08	1.852E-03
Johnson et al. (2021)	420	Algae	<i>Lithophyllum sp.</i>	[mmol/g/hr]	linear +	Positive	0	0.1	1.136E-01
Johnson et al. (2018)	99	Algae	<i>Lithophyllum sp.</i>	[mmol/cm-2]	neutral	Neutral			
Vasquez-Elizondo et al. (2015)	4	Algae	<i>Lithothamnion sp.</i>	[mmol/m-2/hr]	neutral	Neutral			
Ries et al. (2009)	42	Gastropod	<i>Littorina littorea</i>	[mmol/g/hr]	linear +	Positive	0	0.34	1.720E-04
Raymond et al. (2013)	179	Foraminifera	<i>Marginopora rossi</i>	[%/hr]	linear +	Positive	0	0.19	8.962E-03
Prazeres et al. (2015)	47	Foraminifera	<i>Marginopora vertebralis</i>	[%/hr]	linear -	Negative	0.001	0.33	5.481E-04
Uthricke and Fabricius et al. (2012)	47	Foraminifera	<i>Marginopora vertebralis</i>	[mmol/g/hr]	linear +	Positive	0	0.27	4.304E-04
Sinutok et al. (2011)	16	Foraminifera	<i>Marginopora vertebralis</i>	[mmol/hr]	neutral	Neutral			
Ries et al. (2009)	25	Mollusks	<i>Mercenaria mercenaria</i>	[mmol/g/hr]	exponential +	Positive	0	0.83	2.880E+11
Bove et al. (2020)	65	Coral	<i>Montastraea cavernosa</i>	[mmol/m-2/hr]	linear +	Positive	0.015	0.09	5.047E-01
Ries et al. (2009)	14	Mollusks	<i>Mya arenaria</i>	[mmol/g/hr]	linear +	Positive	0	0.73	3.375E-04
Ninokawa et al. (2019)	13	Mollusks	<i>Mytilus californianus</i>	[mmol/m-2/hr]	neutral	Neutral			
Ries et al. (2009), Gazeau et al. (2007)	86	Mollusks	<i>Mytilus edulis</i>	[mmol/g/hr]	linear +	Positive	0.012	0.07	1.739E-04
Gazeau et al. (2014)		Mollusks	<i>Mytilus galloprovincialis</i>	[mmol/m-2/hr]	neutral	Neutral			
Garilli et al. (2015)		Mollusks	<i>Nassarius corniculatus</i>	[mmol/g/hr]	neutral	Neutral			
Manno et al. (2012)	192	Foraminifera	<i>Neogloboquadrina</i>	[mmol/m-3/hr]	linear +	Positive	0	0.71	1.180E+09
Monserrat et al. (2022)	62	Algae	<i>Neogoniolithon brassica-</i>	[mmol/m-2/hr]	neutral	Neutral			
Vasquez-Elizondo et al. (2015), Comeau et al. (2013)	26	Algae	<i>Neogoniolithon sp.</i>	[mmol/m-2/hr]	neutral	Neutral			
Ries et al. (2009)	42	Algae	<i>Neogoniolithon sp.</i>	[mmol/g/hr]	parabolic	Negative	0	0.41	3.301E-04
Ries et al. (2009)	54	Coral	<i>Oculina arbuscula</i>	[mmol/g/hr]	exponential +	Positive	0	0.86	9.680E+10
Oron et al. (2020)	96	Foraminifera	<i>Operculina ammonoides</i>	[mmol/g/hr]	linear -	Negative	0.003	0.09	1.719E-03
Comeau et al. (2013)	72	Coral	<i>Pavona cactus</i>	[mmol/m-2/hr]	exponential +	Positive	0	0.21	9.124E-01
Cameron et al. (2019)	30	Mollusks	<i>Pecten maximus</i>	[mmol/g/hr]	neutral	Neutral			
Ries et al. (2009)	12	Crustacean	<i>Penaeus plebejus</i>	[mmol/g/hr]	linear -	Negative	0.012	0.48	6.279E-04
Comeau et al. (2019)	49	Coral	<i>Plesiothoa verticillata</i>	[mmol/m-2/hr]	linear +	Positive	0.007	0.15	6.003E-01
Casareto et al. (2009)	14	Coccolithophore	<i>Pleurochrysis carterae</i>	[mmol/m-3/hr]	neutral	Neutral			
Brown et al. (2022)	4	Coral	<i>Pocillopora damicornis</i>	[mmol/g/hr]	neutral	Neutral			
Cornwall et al. (2018), Pagan Garcia et al. (2015), Comeau et al. (2013)	117	Coral	<i>Pocillopora damicornis</i>	[mmol/m-2/hr]	neutral	Neutral			
Evensen-Edmunds et al. (2016)	60	Coral	<i>Pocillopora verrucosa</i>	[mmol/m-2/hr]	linear +	Positive	0.013	0.1	0.82969291
Agostini et al. (2021)	35	Coral	<i>Porites heronensis</i>	[mmol/m-2/hr]	neutral	Neutral			
Camp et al. (2017)	2	Coral	<i>Porites lutea</i>	[mmol/m-2/hr]	neutral	Neutral			
Comeau et al. (2013)	72	Coral	<i>Porites rus</i>	[mmol/m-2/hr]	linear +	Positive	0.002	0.13	2.028E+04
Biggs-Capener et al. (2019), Johnson et al. (2014)	431	Algae	<i>Porolithon onkodes</i>	[mmol/m-2/hr]	linear +	Positive	0.001	0.03	8.093E-01
Tatters et al. (2013)	45	Dinoflagellate	<i>Prorocentrum micans</i>	[1/hr]	neutral	Neutral			
Hansen et al. (2007)	21	Dinoflagellate	<i>Prorocentrum minimum</i>	[mmol/#/h]	exponential -	Negative	0	0.88	1.877E-03
Findlay et al. (2010)	6	Crustacean	<i>Semibalanus balanoides</i>	[mmol/g/hr]	neutral	Neutral			
Okazaki et al. (2013)	75	Coral	<i>Siderastrea radians</i>	[mmol/m-2/hr]	linear +	Positive	0	0.16	2.788E+03
Okazaki et al. (2013)	64	Coral	<i>Solenastrea hyades</i>	[mmol/m-2/hr]	exponential +	Positive	0	0.23	2.038E+03
Comeau et al. (2010), Comeau et al. (2019)	64	Algae	<i>Sporolithon durum</i>	[mmol/m-2/hr]	exponential +	Positive	0.007	0.15	1.751E-01
Ries et al. (2009)	21	Gastropod	<i>Strombus alatus</i>	[mmol/g/hr]	exponential +	Positive	0	0.7	8.77E+10
Krueger et al. (2017)	36	Coral	<i>Stylophora pistillata</i>	[mmol/m-2/hr]	neutral	Neutral			
Brading et al. (2011)	175	Dinoflagellate	<i>Symbiodinium sp.</i>	[#/hr]	linear -	Negative	0.001	0.06	6.632E-03
Florini et al. (2011)	2	Coccolithophore	<i>Syracosphaera pulchra</i>	[mmol/#/hr]	neutral	Neutral			
Van de Waal et al. (2013)	12	Dinoflagellate	<i>Thracosphaera heimii</i>	[mmol/m-3/hr]	parabolic	Negative	0	0.85	8.16E+07
Ries et al. (2009)	33	Gastropod	<i>Urosalpinx cinerea</i>	[mmol/g/hr]	linear +	Positive	0	0.57	8.67E+09



338 Such responses could be further summed up into positive (linear and threshold positive), negative
 339 (linear and threshold negative, parabolic) and neutral responses (Fig. 7) when generalized across
 340 the calcification rate against the TA:DIC ratio. Such a summary of responses shows 39.5% species
 341 to respond positively (N=38), 21% species to respond negatively (N=20), while 39.5% showed a
 342 neutral response (N=38).



343
 344 **Figure 6:** Categories of calcification rate responses and percentage (%) response across eleven
 345 groups (calcifying coralline algae, annelids, coccolithophores, corals, crustaceans,
 346 dinoflagellate, echinoderms, foraminifera, gastropods, mollusks, pteropods). The number on the
 347 bar indicates the number of studies of species included.



348
 349 **Figure 7:** Summary of percentage (%) responses in calcification rates as positive (linear and
 350 threshold positive), negative (linear and threshold negative, parabolic) and neutral across
 351 eleven groups (calcifying algae, annelids, coccolithophores, corals, crustaceans, dinoflagellate,



352 *echinoderms, foraminifera, gastropods, mollusks, pteropods*). The number on the bar indicates
353 the number of studies with species included.

354 3.5 Evaluating responses to NaOH/Na₂CO₃ additions

355 Upon added TA, the calcification rate in positive responders will increase, either in a linear or
356 threshold positive response, where calcification plateaus at some point, depending on the species-
357 specific rate of response (Figs. 1, 2, Supplementary Fig. 2). The negative responders (linear or
358 threshold negative and parabolic) will be negatively impacted as follows: first, for the linear
359 negative responders, addition of the Na₂CO₃ will linearly decrease calcification rate, but there is
360 no associated threshold to it; second, for the threshold negative responders, calcification rate will
361 decline in an exponential way until reaching a DIC:TA value, where the response plateaus; third,
362 for the parabolic responders, the calcification rate will initially increase until reaching certain
363 TA:DIC threshold upon which calcification starts declining. We conclude that all the TA:DIC
364 thresholds for negative responders will be species-specific (Table 2).

365 3.6 Threshold values indicative of negative biological response to OAE

366 The metrics to evaluate the sensitivity of calcification rate of the negative responders in this study
367 were based on the amount of NaOH or Na₂CO₃ addition required to reduce calcification rate to a
368 half. The greater the TA:DIC ratio value to trigger half calcification rate reduction, the less
369 sensitive species was to NaOH addition (Table 2). The lowest TA:DIC ratio value was found for
370 the species with parabolic and linear negative responses, followed by those with an exponential
371 negative response. The lowest TA:DIC sensitivities ranged from 10 to 100 μmol/kg of NaOH
372 additions, demonstrated for echinoderms, mollusks and red coralline algae. In the range of NaOH
373 additions of 200–500 μmol/kg, dinoflagellates, coccolithophores, crustaceans, green calcifying
374 and foraminifera were found (Supplementary Fig. 2, Table 2).

375 **Table 2:** *Studies with negative responders (linear and threshold negative, parabolic) with*
376 *demonstrated TA:DIC thresholds, indicating the amount for NaOH or Na₂CO₃ needed to reduced*
377 *calcification rate to half. The value for the TA:DIC threshold is related to the aragonite saturation*
378 *state.*



Studies	Species	Group	Response	NaOH (in $\mu\text{mol/kg}$) treatment	TA:DIC at the NaOH Threshold	Ω_{ar} at the NaOH Threshold	Na ₂ CO ₃ (in $\mu\text{mol/kg}$) treatment2	TA:DIC at Na ₂ O ₃ Threshold
Ries et al. (2009)	<i>Arbacia punctulata</i>	Echinoderm	parabolic	10	1.103	2.31	1.108	50
Ramajo et al. (2016)	<i>Argopecten purpuratus</i>	Mollusks	linear -	100	1.111	2.48	1.114	250
Ries et al. (2009)	<i>Panaeus plebejus</i>	Crustacean	linear -	200	1.117	2.61	1.116	450
Ries et al. (2009)	<i>Homarus americanus</i>	Crustacean	linear -	250	1.143	3.17	1.127	500
Ries et al. (2009)	<i>Neogoniolithon sp.</i>	Algae	parabolic	100	1.175	3.88	1.168	200
Ries et al. (2009)	<i>Callinectes sapidus</i>	Crustacean	linear -	350	1.194	4.30	1.127	500
Hansen et al. (2007)	<i>Caratium lineatum</i>	Dinoflagellate	exponential -	200	1.197	4.37	1.197	500
Prazeres et al. (2015)	<i>Amphistegina lessonii</i>	Foraminifera	parabolic	250	1.199	4.41	1.178	500
Barcelos-Ramos et al. (2010), Fiorini et al. (2011), Iglesias-Rodrigues et al. (2008), Richier et al. (2011), Stoll et al. (2012), Sciandra et al. (2003)	<i>Emiliana huxleyi</i>	Coccolithophore	parabolic	200	1.217	4.81	1.215	500
Wang et al. (2019)	<i>Karenia mikimotoi</i>	Dinoflagellate	linear -	300	1.246	5.45	1.197	500
Van deWaal et al. (2013)	<i>Thoracosphaera heimii</i>	Dinoflagellate	parabolic	300	1.246	5.45		
Meyer et al. (2016)	<i>Halimeda macroloba</i>	Algae	linear -	350	1.275	6.06		
Oron et al. (2020)	<i>Operculina ammonoides</i>	Foraminifera	linear -	500	1.315	6.85		
Brading et al. (2011)	<i>Symbiodinium sp.</i>	Dinoflagellate	linear -	450	1.32	6.94		
Comeau et al. (2013)	<i>Halimeda macroloba</i>	Algae	parabolic	500	1.347	7.42		

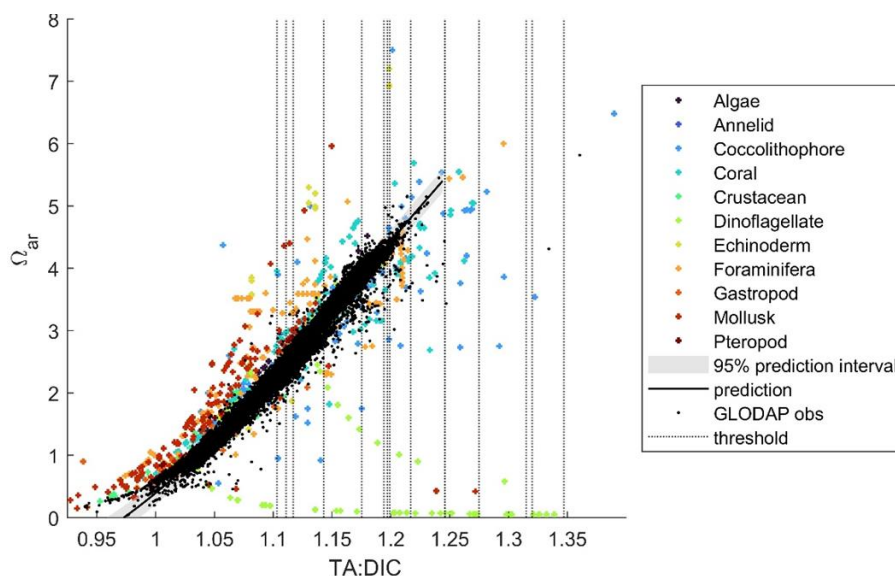
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380

381 3.7 Applications of the TA:DIC thresholds related to added NaOH/Na₂CO₃

382 The DIC:TA thresholds associated with NaOH or Na₂CO₃ addition were applied to assess over
 383 what carbonate chemistry conditions and species' habitats the negative biological effects of OAE
 384 deployment might happen. We extracted Ω_{ar} vs TA:DIC conditions of the upper 50 m of the water
 385 column characteristic for the global ocean conditions, which were derived from the GLODAP
 386 dataset and overlaid TA:DIC thresholds for the negative responders and associated amounts of
 387 NaOH dosing on top (Fig. 8). We emphasize that we used global data to showcase the application
 388 of the thresholds but note that the crossing of the thresholds will be regionally specific.

389 Some of the TA:DIC thresholds are in the range of 1.108 to 1.2, triggered by lower, i.e. 10–200
 390 $\mu\text{mol/kg}$ NaOH additions, indicating the most sensitive species of the echinoderm *Arbacia*
 391 *punctulata*, crustacean *Panaeus plebejus* and mollusks *Argopecten purpuratus* (Table 2). Most of
 392 the thresholds are in the upper range of the observational data, i.e. the TA:DIC of 1.2 and 1.25,
 393 triggered by the additions of 250–350 $\mu\text{mol/kg}$ of NaOH. This suggests that for some species a
 394 very low dosing is needed to cross the biological threshold in their respective habitats to negatively
 395 impact species' calcification rate. Thirds group of TA:DIC thresholds is positioned between 1.25
 396 to 1.35, indicating species that are less sensitive to TA addition, even for additions of \sim 500
 397 $\mu\text{mol/kg}$ NaOH.



398

399 **Figure 8:** Global representation of TA:DIC and Ω_{ar} data from GLODAP covering the upper 0-50
 400 m depth with the fitted curve, overlaid with the experimental data (Figure 4) of eleven groups
 401 from the OA studies with overlaid TA:DIC thresholds associated with the addition of various
 402 NaOH dosing (Table 3).

403

404 4. Discussion

405 OAE is a quickly developing strategy that is already in the field-testing phase despite extremely
 406 limited understanding of potential biological implications and environmental concerns. Hence,
 407 gaining insights of potential risks for the biological species and communities is essential and
 408 timely. In retrospect, it took several decades for the OA research community to get a more accurate
 409 and comprehensive understanding and predictions of biological responses to OA (Gattuso and
 410 Riebesell, 2015). Without a very clear conceptual strategy for the OAE testing, time scales and
 411 efforts might be comparable. Consequently, there is an essential need to develop a conceptual
 412 framework of predictive responses and testing appropriate to OAE, while will assist in OAE
 413 scaling while avoiding potential risks. This paper aims at developing such a framework, where
 414 responses are categorized per species responses against TA:DIC, which helps determine the levels
 415 of TA additions and also related thresholds.

416 4.1. Identified strengths and limitations of the synthesis approach based on OA studies

417 Prior to conducting this study, several drawbacks were identified that potentially limit such an
 418 undertaking: first, insufficient amount of data at the upper range of carbonate chemistry conditions
 419 (high pH, high Ω_{ar}); second, experimental data under conditions with no relevance to natural
 420 settings (Figs. 4, 8); and third, an insufficient number of validation studies under high TA



421 conditions to validate the results of this meta-analyses study. To overcome the first two limitations,
422 the decision was made to combine multiple OA datasets for a single species with the aim to achieve
423 a greater range in carbonate chemistry conditions, including higher pH, Ω_{ar} experimental values,
424 which should reduce the uncertainty of the predictions. However, combining raw data on species
425 calcification rate proved to be more challenging because even across the same species the reporting
426 of the calcification rates was highly variable. The use of different measuring approaches of
427 calcification rates while conducting OA studies generated data with divergent units that do not
428 allow for the intercomparison of data and results. As different studies for a single species could
429 not be combined, we chose to increase the number of studies and thus, the number of examined
430 species. Based on the response categories from the OA studies (Ries et al., 2009), the hypothesis
431 was that OAE will elucidate same categories of responses, i.e. positive, negative and neutral.
432 Within each of the groups examined, multiple categories of predicted calcification response were
433 found. In this way, we demonstrated that it was possible to develop a useful framework for
434 predicting species-specific OAE responses that can delineate different responders, identify species
435 with greater OAE sensitivity and determine the thresholds where such negative responses could
436 happen.

437 We further propose a TA:DIC ratio as a chemical-biological proxy although TA:DIC does not of
438 itself drive biological sensitivity, but rather captures carbonate chemistry changes (*sensu* Bach et
439 al., 2019). Because TA:DIC and Ω_{ar} are strongly correlated (Fig. 3), such ratios can then be
440 used to explain biological responses, e.g. calcification rate changes. The use of the TA:DIC ratio
441 was also done for practical reasons because the additions of TA and/or DIC could be accounted
442 for more easily.

443 **4.2 Synthesizing biological response under OAE additions identifies winner and losers**

444 The greatest certainty in predicting OAE response is possible in species with known calcification
445 mechanisms and parameters involved in this, while the highest uncertainty is related to the groups
446 with unknown calcification mechanisms and where OA experiments did not provide any data at
447 the higher TA:DIC levels. In addition, for the neutral responders or groups with no significant
448 correlation between TA:DIC and calcification rates, it is rather uncertain to predict if such
449 responses will be retained under OAE. While parabolic responders show a physiologically
450 understandable parabolic type of dose-response, positioning the TA:DIC values where the
451 threshold occurs is also highly species-specific and potentially uncertain, meaning that it might
452 depend on other environmental parameters.

453 The greatest variability in calcification rate response upon NaOH addition was evident in
454 calcifying algae and dinoflagellates, mollusks, in particular the gastropods, where four to five
455 different categories of responses were found. Such variability confirms that the responses to OAE
456 will be species-specific and is related to various calcification mechanisms across the observed
457 groups. Despite such specificity, the responses were summarized across three emerging groups of
458 responses: positive, negative, and neutral (Fig. 7), which we discuss in the context of possible
459 mechanisms of calcification or available OAE experimental studies used for validation.



460 Positive responders (40%) show increased calcification rate to OAE additions (Fig. 6), observed
461 in corals, annelids, and pteropods. Moreover, these groups have one of the lowest TA:DIC
462 standard deviation intervals, which additionally supports the highest certainty in predicting their
463 responses to OAE. Corals in general show uniformity in positive responses, although the
464 variability is in a type of the response and predicts that coral species would not be negatively
465 impacted during the OAE field trials. For validation purposes, increased coral calcification was
466 also shown by the field experiment conducted by Albright et al. (2016), as well as for two coral
467 species of *Acropora* and *Siderastre* in the experiments conducted by Palmer et al. (2023).

468 The metrics to evaluate the sensitivity of calcification rate for the negative responders (negative
469 linear and threshold) to OAE addition was based on the amount of alkalinity addition required to
470 reduce the calcification rate to a half (Fig. 7, Tables 1, 2). The most negative responses are
471 expected in dinoflagellates (57% species), crustaceans (50% species) and foraminifera (38%). As
472 such, these groups are one of the priorities for the future OAE experimental work to determine at
473 which TA: DIC negative response happens. The worst out of these are dinoflagellates that
474 demonstrate negative response in 6 cases, 5 neutral responses and 0 positive (see Table 1,
475 Supplementary Fig. 2). The reason for negative response to OAE in this group is related to the fact
476 that their growth gets limited at higher pH, with further carbon limitation playing a role at very
477 high pH levels and low DIC concentration (Hansen et al., 2002; 2007). On the other hand,
478 crustaceans only demonstrated positive response in one study (Pansch et al., 2014), while
479 remaining results predict either negative or neutral response. While crustaceans are effective in
480 retaining homeostasis at lower pH, they might be less so at higher pH, which was shown in the
481 OA experiments by Ries et al. (2009) for three crustacean species (*Callinectes sapidus*, *Homarus*
482 *americanus*, *Penaeus plebejus*), confirmed in the OAE study by Cripps et al. (2013) in *Carcinus*
483 *meanas*. Reduced calcification in crustaceans is likely because the bicarbonate ions modulate their
484 metabolic responses (Maus et al., 2018), as well as potential acid-base imbalance at high pH
485 (Tresguerres et al., 2020).

486 With respect to the coccolithophores, we note that this was the only group where data compilation
487 on calcification rate across the groups was possible because the OA studies were conducted in a
488 more uniform way, using similar approaches, and reporting the same units. When data for *E.*
489 *huxleyi* across the comparable studies was compiled (Barcelos-Ramos et al., 2010; Fiorini et al.,
490 2011; Iglesias-Rodrigues et al., 2008; Sciandra et al., 2003; Stoll et al., 2012; Richier et al., 2011),
491 a significant parabolic response was obtained (Supplementary Fig. 2), although the goodness of fit
492 was fairly low ($R^2=0.09$). Despite lower R^2 , we decided to use the compiled dataset because of the
493 increased statistical power. The parabolic response obtained aligns with Langer et al. (2006) and
494 also with the parabolic type responses found in the synthesis study by Paul and Bach (2020) and
495 Bach et al. (2015). The threshold indicates the mechanisms of the coccolithophore growth, which
496 is driven by CO_2 , which is reduced with the OAE treatment. The threshold for coccolithophore
497 combined studies was positioned at TA:DIC at 1.217 ($\Omega_{ar} = 4.81$, Table 2), which would be
498 triggered at 200 $\mu\text{mol/kg}$ of added NaOH on a global level. This is a comparable magnitude to the
499 predicted threshold of phytoplankton growth limitation at 100 μatm for some coccolithophore
500 species (Riebesell et al., 1993). It is important to note that when these studies were analyzed



501 individually, a mixture of different responses was observed. We emphasize the variability within
502 the coccolithophore responses, which are species-specific and inherently related to the strain
503 adaptation to their innate regional settings and dependent on a variety of other factors (Bach et al.,
504 2015; Gafar and Schultz, 2018), including the longevity of the species, the experimental settings
505 used in the study, for example nutrient-replete vs nutrient deficient conditions, and the presence or
506 absence of (un)suitable light conditions. Interestingly, for other than *E. huxleyi* species, all the
507 other coccolithophores demonstrated neutral responses. For validation purposes, the results of our
508 study could not be compared to Gately et al. (2023) because calcification rates were not studied,
509 and it is urgent that more validation studies for coccolithophores are conducted.

510 **4.3 TA:DIC thresholds related to biological sensitivity**

511 Lastly and most importantly, a set of species-specific thresholds was developed in this study, with
512 demonstrated application across the global Ω_{ar} vs TA:DIC conditions (Table 2, Fig. 8). We limited
513 the upper threshold value to 500 $\mu\text{mol/kg}$ because the biogeochemical model outputs show that
514 while the OAE-related concentration at the injection site might be higher for a short-time, realistic
515 field dosing upon dilution might be low. Wang et al. (2023) reported that the nearfield maxima in
516 the respective investigation area of the Bering Sea is to increase TA by about 10 $\mu\text{mol/kg}$ and
517 farfield by about 1 $\mu\text{mol/kg}$ of NaOH (Wang et al., 2023).

518 The TA:DIC thresholds upon TA application ranged between 10–500 $\mu\text{mol/kg}$ of NaOH, pointing
519 to the most and least species-specific OAE-related sensitivities, respectively. The lowest TA:DIC
520 threshold is predicted for the echinoderm *Arbacia punctulata*, with the sensitivity value being at
521 least an order of magnitude lower than what the lab experimental OAE trials use in their treatment
522 levels. While the lab experiments aim to gain mechanistic understanding of the OAE response,
523 such high treatment levels are not very realistic with respect to potential level of biological
524 sensitivity in the field. Here, we explicitly emphasize the importance of including much lower
525 additions of TA as the experimental treatment levels to better support biological understanding in
526 the field. Prior to the lab experiments it would be important to identify the most sensitive species
527 with negative response with a threshold at lower TA:DIC range. This is especially pertinent for
528 the groups for which OA experimental data is limited and only distributed at the lowest and the
529 mid TA:DIC ratio, such as mollusks and dinoflagellates (Fig. 8; Supplementary Fig. 2).

530 **4.4 Bringing realism of OAE experiments to the field trials**

531 OAE-related biological responses and risks are not going to depend solely on the concentration of
532 OAE compound used but also on the baseline carbonate chemistry conditions at the site of
533 deployment, such as baseline TA:DIC (pH/Ω_{ar}) and variability of carbonate chemistry parameters
534 across horizontal and vertical depths. Physical parameters of importance are related to the dilution
535 effect, mixing, retention capacity, as well as the rate of the equilibration effects of the air-sea CO_2
536 uptake (Ferderer et al., 2022; He and Tyka, 2023; Schulz et al., 2023, Wang et al., 2023).
537 Variability on the seasonal and annual scales of the air-sea CO_2 uptake can have impacts not only
538 on the chemical processes related to the variable OAE efficiency, but also for the biological
539 implications related to the crossing of biologically sensitive thresholds. It is the combination of all



540 these factors that creates baseline conditions to which biota would ultimately be exposed in their
541 natural environment upon OAE deployment (Wang et al., 2022).

542 If similar conditions as induced by the OAE field trial are present as part of the natural variability
543 within the species' habitat, it is more likely that the species might be adjusted to it. On the contrary,
544 rapidly induced novel conditions might be the most detrimental. As such, it is worth considering
545 if OAE deployments could be, when possible, carried out not as a single high dosage deployment,
546 but rather as a more continuous, lower dosage application that would eliminate the swings and
547 maxima in conditions, while also allowing more time for species acclimation or migration during
548 the initial injection of the OAE deployment.

549 What is needed urgently for the community performing biological field trials is a best practice
550 guide for the biological impact and environmental risk monitoring approach, which is currently
551 missing. While the guidance is available for conducting the lab (Iglesias Rodrigues et al., 2023)
552 and field OAE studies (Cyronak et al., 2023), such guide on the environmental risk assessment
553 should set the framework, establish the baseline conditions, identify suitable risk analyses,
554 determine thresholds, and propose the development of regionally specific indicators for
555 monitoring, while also identify the guidance for the regulators. Ideally, such biological and
556 environmental risk monitoring and assessment would be accompanied by the application of the
557 physical mixing models with site-specific biogeochemical processes (Ho et al., 2023; Fennel
558 et al., 2023) that can predict the maximum expected TA increase in the nearfield and farfield,
559 representing a more realistic exposure and better informing of the further experimental work.

560 **4.5 Unknowns about ecological and biogeochemical implications call for the precautionary** 561 **approach**

562 From an ecological perspective, only 40% of species show neutrality in responses, which indicates
563 that more than half of the examined species are predicted to have either a positive or a negative
564 response. While the implications of a direct negative effect are inherently understood, a positive
565 effect could be ambiguous in its interpretation. Positive responders could indeed benefit directly
566 from the altered conditions induced by OAE in terms of increased calcification, but the indirect
567 implications could be equally important, but are completely unknown at the moment. Would the
568 positive responders benefit in physiological terms, implying they would be ecological winners and
569 could induce a shift on the community level? Substantial species-specific variation in responses to
570 OAE could lead to potential winners and losers, just as expected for the OA or multiple stressors.
571 40% of positive is a significant number related to potential consequences on the community shifts.
572 The idea that the calcifiers are winners and thus there are (co)-benefits for marine calcifiers is not
573 entirely fitting because it does not take the implication of potential ecological shifts into account.
574 Such co-benefiting effects could only be considered within the context of mitigating effects to
575 ocean acidification, i.e. when these species are negatively impacted by OA and OAE would reverse
576 the negative OA pattern. However, current modelling efforts show that temporal and spatial scope
577 of OAE as a mitigation capacity for OA is variable and might induce great biogeochemical changes
578 that further exacerbate ecological risks (González and Ilyina, 2018; González et al., 2016; Mongin
579 et al., 2021).



580 While we identified species with predicted positive and negative responses, we also note that this
581 study did not include diatoms in the analyses, which are predicted to be negatively impacted by
582 the carbonate-based OAE (Ferderer et al., 2022), with potential implications for the community
583 shifts (Bach et al., 2019). Furthermore, this study also did not include any of the non-calcifiers in
584 the analyses, where OAE might potentially trigger even greater implications within the calcifying
585 and non-calcifying community, especially when the grazing effects are included, further
586 strengthening the notion of the winner-loser concept and associated risks. As such, overall non-
587 neutral responses should elucidate similar caution to negative responses and determine a
588 precautionary principle in considering the next steps of OAE field implementation.

589 From the biogeochemical perspective, it could be inferred that OAE will introduce changes in
590 calcification rate across species, potentially resulting in changing carbon export and carbonate
591 counter pump. While species-specific responses in two of the major carbonate producers, i.e.
592 coccolithophores and foraminifera (40%) show a negative response, this could have strong effects
593 on biogeochemical fluxes (Riebesell et al., 2017; Bach et al., 2019). On the contrary, increased
594 calcification could result in thicker and denser shells, contributing to faster sinking and increased
595 carbonate fluxes. Changes in calcification could trigger effects on the subsurface total alkalinity at
596 intermediate and deeper depths in the water column, and dissolution on the seafloor (Gehlen et al.,
597 2011) with potential feedback that results in increased CO₂ flux to the atmosphere (Gattuso et al.,
598 2021), although this is projected to occur over centennial time scales (Oschlies et al., 2023).

599 **4.6 Potential confounding effects not delineated in this study**

600 This study only considered the changes in carbonate chemistry due to the addition of carbonate-
601 based compounds, i.e. NaOH or Na₂CO₃. However, other feedstocks contain compounds that could
602 induce biological toxicity due to the presence of the trace metals (Ni, Cu, Ca, Si; Bach et al., 2019),
603 as well as potential negative environmental impacts due to the secondary precipitation (Hartmann
604 et al., 2022; Moras et al., 2022). It also did not examine the sensitivity across different life stages,
605 even though different sensitivities to OAE based are expected based on OA results. Furthermore,
606 we did not consider the impact of multiple stressors, including temperature, dissolved oxygen,
607 light intensity, although they could elicit different biological pathways than OAE alone or have
608 additional confounding effects. As such, experimental lab or field studies or data that involve
609 multiple stressors in their experimental designs was not used. We note that a similar predictive
610 framework of OAE could, in principle, be placed within the multi stressor conditions given the
611 amount of newly generated studies of the impact of multiple stressors currently.

612 **4.7 Conclusions and next steps**

613 Sufficient certainty in predicting biological responses reduces the risks and supports safe operating
614 space for OAE implementation and scaling up. Overall, given that 60% of examined species
615 showed non-neutral response (either positive or negative), this calls for care in OAE field
616 implementation until the temporal and spatial scales of safe operations are determined and OA
617 mitigation established. The goal of this study is to serve as a baseline for prioritizing experimental
618 and field OAE research and assess environmental risks, eliminating or reducing the risk with the



619 OAE biological field trials. Such prioritization identifies those species for which experimental
620 work needs to be conducted first. This would involve species with the greatest OAE-related
621 sensitivity (negative responders), species with the greatest uncertainty in response, as well as the
622 species with very strong predicted positive response that could potentially introduce a shift on the
623 community level. In addition, it would also recognize the species for which the existing knowledge
624 is sufficient and there is less immediate need for the OAE experiments.

625 It is important to consider this study as a first meta-analyses that should be continuously upgraded
626 and cross-validated with the experimental work. Furthermore, we emphasize that our predictions
627 were developed as calcification response of the pelagic organisms only. Similar OA datasets are
628 available for the benthic calcifiers and non-calcifiers and also for other biological responses,
629 including growth, survival, with much greater uniformity of data and units, that could be easily
630 transformed into OAE predictive framework as proposed in this study.

631

632 **Data availability**

633 No additional data were generated as part of this study, they were all collected from the already
634 published studies. We provide all the information behind the analyzed studies.

635 **Author contributions**

636 NB designed and conceptualized the research, wrote the paper. GP provided the analyses using
637 GLODAP data, provided visualizations and formal analyses. HvdM collected and curated data,
638 conducted formal analyses and provided visualization. MGR has provided formal statistical
639 analyses and visuals. RAF and AD have provided insights, suggestions, and generated discussion
640 about specific parts of the paper. All authors have exchanged numerous insights, mutually
641 contributed to the development of the study, troubleshooting, improvements. All have contributed
642 to the writing of this draft.

643 **Competing interests**

644 The contact author has declared that none of the authors has any competing interests.

645

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