



1 Biological thresholds for marine carbon dioxide removal 2 (mCDR): the effect of changes in carbonate chemistry

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20 **Abstract.** Marine carbon dioxide removal (mCDR) encompasses a variety of approaches to actively
21 remove CO₂ from the atmosphere, which, given current and projected emissions, is necessary to keep
22 global average temperature increases to less than 2°C. In addition to the removal of CO₂ from the
23 atmosphere, mCDR projects would have effects on the marine environment, including changes in ocean
24 carbonate chemistry. These changes in carbonate chemistry can affect marine organisms through multiple
25 physiological pathways. Although research on the effects of ocean acidification over the last fifteen years
26 has advanced understanding of the effects of low pH/high CO₂ conditions on marine organisms, much less
27 is known about organismal response to the high pH/low CO₂ or high alkalinity conditions that can be
28 generated by some mCDR methods. We created a database of available information on marine species
29 response to the carbonate chemistry conditions that can be generated by mCDR with a focus on
30 identifying carbonate chemistry thresholds at which biological responses occur. The database contains 310



31 studies, from which we estimated 276 thresholds. In addition to all mCDR studies available to date, we
32 reviewed studies not explicitly designed to address mCDR. These studies used natural and artificially
33 manipulated variations in carbonate chemistry, including increasing pH and alkalinity, to explore basic
34 physiological and biological responses as well as approaches to mitigate ocean acidification. In analyzing
35 the database, we considered a variety of biological responses, both positive and negative, and considered
36 sensitivity by taxa, exposure duration, treatment method and other factors. Using practical definitions of a
37 threshold, including one based on the treatment level leading to the first statistically significant biological
38 response, we describe the distribution of pH and alkalinity threshold values. The data reveal a high
39 tolerance for high pH (>12) and high alkalinity for some species responses under some experimental
40 conditions, but negative response to experimental conditions only slightly above ambient (pH 8.3) for
41 other species responses. A positive effect of pH above ambient levels was observed in six cases, just 3%
42 of the total. We summarize results by presenting the distributions of threshold estimates collected from
43 individual studies. The uncertainty and variation in organismal response represents a challenge for the
44 development of management guidelines for the developing mCDR industry. Building on our review of
45 existing studies, we suggest several paths forward for improved biological threshold estimates for
46 mCDR-relevant carbonate chemistry conditions.

47 **1 Introduction**

48 **1.1 Overview**

49 This review focuses on identifying the exposure at which marine species become sensitive to the changes
50 in carbonate chemistry generated by marine carbon dioxide removal (mCDR), or, in other terms, putative
51 biological threshold responses. The introduction briefly covers the motivations and methods of mCDR,
52 how mCDR can change seawater carbonate chemistry and how changes in seawater carbonate chemistry
53 can affect basic biological processes. The introduction also explores how thresholds can be defined and
54 discusses these definitions in the context of mCDR management. The bulk of the paper contains a review
55 of the literature describing how different marine species respond to the carbonate chemistry conditions
56 that can be created by mCDR. We collected information for the literature review in a publicly available
57 database that includes 276 threshold estimates extracted from 310 experiments or field observation
58 studies. We provide some summary estimates of the mCDR-like carbonate chemistry conditions that can
59 lead to positive or negative effects on species, with an emphasis on the uncertainty in the estimates and
60 recommendations for additional targeted research.



61 1.2 Marine Carbon Dioxide Removal (mCDR)

62 Achieving the goal of keeping global average temperatures from rising more than 2°C above pre-industrial
63 levels will likely require the removal of ~10 Gt of CO₂ per year from the atmosphere by 2050 (IPCC,
64 2022; Lamb et al., 2024). CDR research, governance, and implementation is most advanced for a few
65 terrestrial approaches, such as afforestation (Fuhrman et al., 2023). However, because of the role of the
66 ocean in the global carbon cycle, there is increasing interest in the potential of marine CDR (mCDR) that
67 utilizes the vast storage potential, large surface area, and specific physical, biological and chemical
68 processes in the ocean (Doney et al., 2024). mCDR technologies (BOX 1) are generally in the early stages
69 of development and no current technologies have demonstrated feasibility to achieve the removal targets
70 outlined above (Ho and Bopp, 2024).

Box 1: mCDR methods

mCDR approaches can be partitioned into biotic and abiotic methods (Doney et al., 2024; Ho and Bopp, 2024; NASEM, 2022). Biotic methods are based on increasing productivity of primary producers, which capture CO₂ through photosynthesis, then sequestering some fraction of the biomass (with its captured CO₂) for long-term storage, typically in the deep ocean. Primary production can be increased either by fertilization of the ocean surface to stimulate phytoplankton production (e.g., with the addition of iron or by using artificial upwelling), through aquaculture production of macroalgae or, to a limited extent, through recovery of marine ecosystems. Sequestration of the carbon-rich biomass created by increased primary production would happen through natural sinking in the case of fertilized phytoplankton. Artificial downwelling could also potentially be used to assist in the downward transport of phytoplankton enhanced by fertilization or from regions that are naturally productive. Macroalgae approaches would generally require active approaches to sink biomass (e.g., ballasting).

There are two general approaches to abiotic mCDR, 1) ocean alkalinity enhancement (OAE) and 2) electrochemical engineering with direct ocean carbon capture and sequestration (DOCCS). With OAE, alkaline material is added to the surface ocean, which raises the surface pH, allowing the ocean to absorb and retain more CO₂ from the atmosphere. The alkaline material can be either from natural minerals mined on land (e.g., olivine), chemicals processed from minerals (e.g., quicklime [CaO]), or generated using electrochemical methods that produce alkaline solutions to add to seawater. With DOCCS, CO₂ is removed directly from seawater in the surface ocean, often using electrochemical techniques, which allows the ocean to absorb more CO₂ from the atmosphere. It is often proposed that



the CO₂ collected by direct ocean capture be sequestered in the deep ocean, though alternative sequestering approaches may be possible.

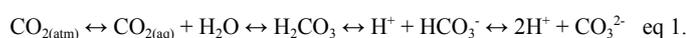
71 The long-term goal of mCDR is to decrease the concentration of CO₂ in the atmosphere and therefore limit
72 increases in global temperature and, as a potential co-benefit, mitigate ocean acidification (OA). Limiting
73 temperature increases and reducing OA would have important beneficial consequences for marine
74 ecosystems and fisheries (Cooley et al., 2022). The climate mitigating effects of mCDR on marine
75 ecosystems will only accrue over timescales of decades when mCDR is implemented at scale and in
76 combination with other actions (i.e., emission reductions). However, on shorter timelines, implementing
77 mCDR is likely to have effects on marine ecosystems that go beyond those driven by mCDR's effect on
78 climate. For example, some biotic approaches seek to change species abundance and composition at the
79 base of the marine food web at a scale that affects global carbon dynamics; this could have major effects
80 on ecosystem processes. Similarly, OAE involves the addition of minerals or alkaline chemicals to the
81 ocean, which may contain harmful compounds, or settle on benthic habitats (Flipkens et al., 2021).
82 Electrochemical approaches for OAE or direct ocean capture require large amounts of electricity
83 (NASEM, 2022), which may be most efficiently generated on or near the ocean, leading to a variety of
84 possible coastal ecosystem effects (Copping and Hemery, 2020; Watson et al., 2024). Any of the methods
85 may require the addition of physical infrastructure or lead to increased ship traffic in the ocean (Caserini et
86 al., 2021; Grabb et al., 2025). These and many other potential non-climate cumulative effects of mCDR on
87 marine ecosystems have been described in a number of studies and reports (Grabb et al., 2025;
88 Gurney-Smith, 2026; Jewett et al., 2026).

89 All of the mCDR methods are generally capable, at least potentially, of generating carbonate chemistry
90 conditions outside the range that naturally occurs in the ocean, which currently has a mean pH ~8.1 (BOX
91 2). For example, OAE could be conducted by the dispersal of concentrated NaOH (sodium hydroxide, a
92 strong base; pH ~14) into the ocean, which would result in some high pH increases at the point of
93 discharge (Caserini et al., 2021). Direct ocean capture methods are capable of removing nearly all the CO₂
94 from seawater, which results in CO₂ and pH values seldom observed in the ocean (pH > 9). Even the biotic
95 mCDR methods, which rely on the natural process of photosynthesis, can result in low CO₂/high pH
96 conditions in locations and for sustained periods of time that would not naturally occur (Brussaard et al.,
97 1996; Middelboe and Hansen, 2007; Wu et al., 2025). Although extreme high pH or low CO₂ conditions
98 are conceptually possible with mCDR, mixing, dilution, and precipitation will tend to constrain the spatial
99 and temporal extent of species exposure to these conditions (Khangaonkar et al., 2024).

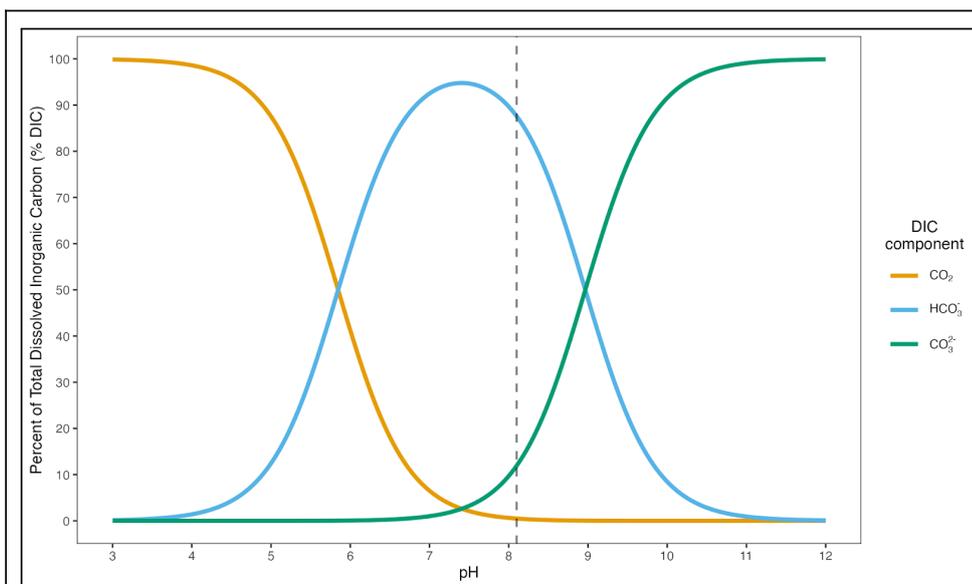


Box 2: mCDR and carbonate chemistry

All mCDR methods manipulate ocean carbonate chemistry, which may have effects on marine species and ecosystems. The fundamental ocean carbonate system is described by a simplified set of equilibria of dissolved inorganic carbon (DIC) (NASEM, 2022) (Eq 1).

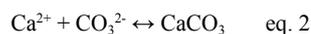


The equilibrium state of the system is determined by the concentrations of the components of the system and the pH (Box 2 Figure). Because the concentration of the DIC components both affects and is affected by the pH, the equilibrium state after perturbation of DIC components or pH is not always intuitively obvious. The directional change caused by four important perturbations (OA, DOCCS, OAE, and calcium carbonate precipitation) is shown in the box 2 table (Doney et al., 2009; NASEM, 2022). OA is caused by adding CO_2 to the system, primarily from the burning of fossil fuels, and results in lower pH and lower carbonate concentrations, both of which can have important negative biological consequences (Doney et al., 2020; Findlay et al., 2025). CO_2 can be removed from the system by biotic mCDR or DOCCS. With biotic mCDR, CO_2 is removed by photosynthesis which converts CO_2 to organic carbon compounds, a fraction of which are then sequestered. With DOCCS, electrochemical or membrane methods are used to remove CO_2 . The removal of CO_2 results in higher pH and carbonate concentrations – the opposite of OA. OAE uses the addition of alkaline chemicals or minerals to increase seawater pH. This pushes the system to overall higher DIC, with a particular effect of increasing bicarbonate (HCO_3^-) and reducing CO_2 . Because mCDR counters many or all of the carbonate chemistry changes produced by OA, mCDR has been proposed as a direct mitigation strategy for OA as well as climate change.



Box 2 Figure: The percent of dissolved inorganic carbon (DIC) components as a function of pH. Calculated with the dissociation constants of Lueker et al. (2000) at a temperature of 25°C and a salinity of 35 psu using functions in the R Seacarb package (Gattuso et al., 2024). The vertical dashed line shows the approximate current surface ocean pH (8.1).

It can take some time for the carbonate system described in equation 1 to reach equilibrium after a perturbation. Depending on the particular mCDR process and species distribution and behavior, an organism may be exposed to equilibrated or non-equilibrated conditions. In particular, equilibration rate (and marine species) can be affected by the formation of precipitates. As seawater pH or calcium carbonate saturation state (Ω) increase, brucite ($\text{Mg}(\text{OH})_2$), calcium carbonate (CaCO_3) and other -compounds may precipitate out of solution (Moras et al., 2022; Suitner et al., 2024a). These precipitates may have direct biological effects on species, but it will also lead to additional changes in the carbonate system (Box 2 table). Consider the precipitation of calcium carbonate (Eq. 2).



The formation of solid calcium carbonate reduces the concentration of dissolved carbonate as a component of DIC, which pushes the system to a new equilibrium with a lower pH. The formation of calcium carbonate can be a relatively slow process and reaching a new equilibrium after the start of



precipitation can take hours, days or weeks, depending on the temperature, pH, presence of nucleating material and other factors. This is important from the perspective of understanding biological response because species may experience equilibrium or non-equilibrium conditions for varying periods of time. For example, the addition of a highly alkaline material (e.g., concentrated sodium hydroxide [NaOH]) may result in a large immediate increase in pH followed by a slow reduction in pH if conditions lead to precipitation.

Box 2 table: Direction of change for components of the ocean carbonate chemistry system from three types of perturbation (ocean acidification, CO₂ removal, and alkalinity enhancement). The up arrows indicate an increase in the component, the down arrows a decrease and the dashes no change. The OA column applies to the process of CO₂ addition to the ocean, not necessarily lab manipulations to simulate OA. The OAE (equilibrium) column applies to situations where equilibration with the atmosphere has occurred in the ocean. As indicated by the asterisk (*) in the table, at equilibrium and to the extent that OAE causes CDR, the pCO₂ in the ocean and atmosphere will be slightly less than before alkalinity addition. The OAE (pre-equilibrium) column applies to the condition immediately after addition of a base like NaOH. The pre-equilibrium state will differ from that shown in the table if the alkaline material is carbonate based (e.g. CaCO₃ or Na₂CO₃) and for some other types of materials (e.g., olivine). The changes in the table are based on an assumption of average global ocean surface temperature, salinity and initial pH.

Parameter	OA	Remove CO ₂ (DOCCS or photosynthesis)	OAE (Equilibrium)	OAE (Pre- Equilibrium)	Abiotic Calcification
pCO ₂	↑	↓	*	↓	↑
[H ⁺]	↑	↓	↓	↓	↑
pH	↓	↑	↑	↑	↓
[HCO ₃ ⁻]	↑	↓	↑	↓	↓
[CO ₃ ²⁻]	↓	↑	↑	↑	↓
DIC	↑	↓	↑	—	↓
ALK	—	—	↑	↑	↓
Ω	↓	↓	↑	↑	↓



100 Optimizing carbon removal efficiency will drive constraints on the design of mCDR changes in carbonate
101 chemistry. For example, the precipitation of calcium carbonate greatly reduces the efficiency of OAE
102 (Moras et al., 2024; Ringham et al., 2024; Suitner et al., 2024b), so mCDR developers try to avoid high
103 pH conditions that can lead to precipitation. Some abiotic approaches pump water into a facility for
104 processing, then discharge water that is near equilibration with the atmosphere, which reduces swings in
105 the carbonate chemistry of water entering the ocean (Hartmann et al., 2023; Suitner et al., 2024b).
106 Although these various constraints and approaches may limit the extent of extreme changes in carbonate
107 chemistry, all of the mCDR methods create carbonate chemistry conditions that are different from the
108 current ocean. This is fundamental to how mCDR works – CO₂ removal from the atmosphere requires
109 some changes in ocean carbonate chemistry.

110 1.3 mCDR carbonate chemistry effects on organisms

111 Several decades of laboratory research on the biological effects of OA have shown that organisms can be
112 negatively affected by the low pH and low carbonate ion conditions created by increased ocean uptake of
113 atmospheric CO₂. Much less is known about the biological consequences of the carbonate chemistry
114 conditions caused by mCDR. Different biological processes may be affected by changes in multiple
115 components of the carbonate system (Table 1). Changes in pCO₂; concentrations of H⁺, HCO₃⁻ and CO₃²⁻;
116 and calcium carbonate saturation state can affect biological functions like photosynthesis (which relies on
117 CO₂ and HCO₃⁻), calcification (which relies mostly on HCO₃⁻), reproduction (sensitive to pH), nitrogen
118 fixation (particularly affected by pH), respiration (affected by pH), and precipitation versus dissolution of
119 calcium carbonate (governed by calcium carbonate saturation state) (Andersson and Gledhill, 2013; Bach,
120 2015; Doney et al., 2009; Esbaugh, 2018; Hong et al., 2017; Ninokawa et al., 2024; Ries et al., 2009).
121 Changes in pH, CO₂, and HCO₃⁻ can influence key physiological processes in animals, including
122 enzymatic activity, acid–base regulation, and transport of ions, metabolites, and wastes (e.g., ammonia)
123 across respiratory surfaces respiratory surfaces (e.g., gills, body surface, or specialized epithelia) and
124 within internal fluids (extracellular and intracellular), as organisms adjust to maintain homeostasis under
125 changing external conditions (Brauner and Baker, 2009; Gilmour and Perry, 2009; Hu et al., 2018; Wilkie
126 and Wood, 1991).

127 **Table 1:** Key carbonate parameters that affect fundamental biological processes. Although this table
128 highlights key pathways, it is important to note that the carbonate parameters are not independent (eq 1)
129 and biological processes are complex and prone to exceptions, so this table presents a generalized
130 simplification. A check indicates an effect of the parameter on the biological process, not the direction of



131 change. Dissolution is unlikely to be affected by mCDR because mCDR tends to increase carbonate
 132 concentration and Ω , however it is included for completeness.

Biological Process	pH	CO ₂	HCO ₃ ⁻	CO ₃ ²⁻	Ω	CaCO ₃
Enzyme kinetics	✓	✓	✓			
Internal acid/base balance	✓	✓	✓			
Membrane transport	✓	✓	✓			
Physical disruption						✓
Photosynthesis	✓	✓	✓			
Calcification	✓		✓			
Dissolution				✓	✓	
Fertilization	✓					

133

134 Biological reactions can be extremely sensitive to pH, and organisms tend to have an optimal pH range
 135 above or below which they will experience sublethal degradation and ultimately death. Although some
 136 marine alkaliphilic bacteria can live in pH as high as 12.5 (Gutleben et al., 2025), most organisms have a
 137 lethal limit substantially below this pH level. Although natural selection would generally result in marine
 138 organisms having pH optima near the current conditions of their environment, the optimal pH for some
 139 marine organisms and functions may be above current ocean pH levels. This may be because the current
 140 ocean has already experienced substantial OA and organisms evolved for pre-industrial pH, or because of
 141 other processes that can cause an organism to not be optimally matched to its environment (Crespi, 2000).

142 Depending on their mechanism of carbon capture, photosynthesising organisms can use either CO₂,
 143 HCO₃⁻, or both as a carbon source, although nearly all photosynthetic marine organisms have developed a
 144 carbon concentrating mechanism (Reinfelder, 2011). Thus, decreases in pCO₂ from direct ocean capture or
 145 increases in [HCO₃⁻] from OAE would tend to have opposite effects on primary production (Bach et al.,
 146 2013). This carbon resource effect would be in combination with any pH-driven effects on other
 147 physiological processes. HCO₃⁻ is the source of carbon for calcification in most calcifiers, and higher
 148 HCO₃⁻ concentration seems to promote calcification in almost all marine calcifiers including corals

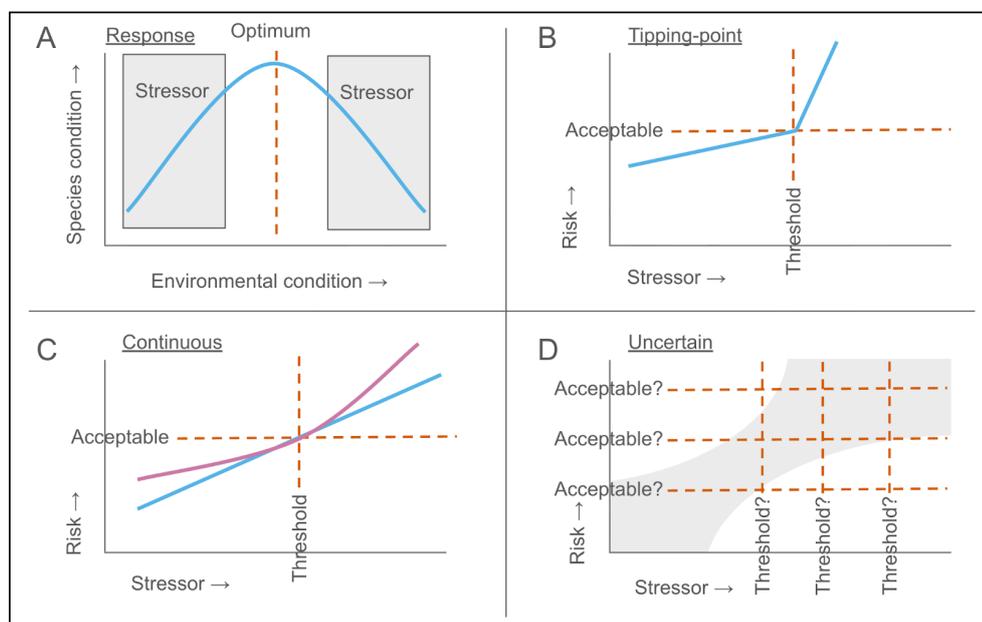


149 (Herfort et al., 2008; Tinoco et al., 2023), echinoderms (Dupont et al., 2010) and phytoplankton
150 (Iglesias-Rodriguez et al., 2008; Ries et al., 2009).

151 1.4 Biological thresholds

152 Biological thresholds can be described as the environmental condition at which the biological response of
153 a species (or ecosystem) induces a qualitatively different state (Figure 1). Thresholds can be used in a
154 management context to set regulatory limits or drive other management actions. The scientific challenge is
155 in determining the relationship between environmental stress conditions and species response. The policy
156 challenge is in deciding what species response constitutes an unacceptable risk. This review focuses on the
157 scientific question of species response to mCDR carbonate chemistry conditions and does not weigh in on
158 regulatory and societal questions that involve (un)acceptable risk.

159



160

161 **Figure 1:** Conceptual diagrams of the relationship between environmental conditions, species condition,
162 stressors, thresholds and acceptable risk. Panel A shows a common species response to environmental
163 conditions in which there is an environmental condition that results in optimum performance, and in
164 which the species performs less well if the environment is above or below the optimum (stressor state). As



165 the stressor becomes more severe, species response could follow several function forms: tipping point (B),
166 linear continuous (C; blue line) or non-linear continuous (C; purple curve). Identifying a threshold for
167 management purposes requires associating species performance with an acceptable level of risk. In
168 practice, there is often imperfect information about the shape of the species response curve (e.g. could be
169 any shape in the grey shaded area of panel D) and an ill-defined acceptable level of risk (multiple
170 horizontal lines in panel D), with both input types of uncertainty leading to uncertainty in where to
171 establish management thresholds.

172 Identifying biological thresholds can be extremely challenging because there may, in fact, not be an
173 environmental condition that leads to a qualitatively different state (Figure 1 panel C). For example,
174 probability of death may be a continuous function of pH, in which case selecting a single pH value as a
175 threshold is somewhat arbitrary. In practice, simplifying assumptions (e.g., first detection of response) and
176 established conventions (e.g., Lethal Concentration 50%) can generate threshold estimates even in the face
177 of limited data on the shape of the response curve. Although this paper is focused on biological thresholds
178 and not management, it is useful to consider the context for our review (BOX 3).

Box 3: Thresholds in mCDR management

Biological and ecological thresholds are often used as a basis for establishing regulatory limits, as inputs for spatial planning, and other marine management decisions (Foley et al., 2015; Hiddink et al., 2023; Hitchin et al., 2023; Kelly et al., 2015; McKellar et al., 2025; Samhouri et al., 2010). In general, management thresholds should be easy to understand, based on readily measurable and cost-effective indicators, have a well-understood link to species or ecosystem response, and can discriminate changes in the system. For mCDR, there is a potential to set initial thresholds for environmental impacts before the commencement of large-scale commercial activities (Johnson et al., 2024).

Relevant to mCDR, pH thresholds in water quality regulations have been in use for nearly 50 years with the intent to protect public health and the environment (Bach et al., 2025). The U.S. Environmental Protection Agency's recommended pH criteria for marine aquatic life is 6.5 to 8.5 (USEPA, 1976) and states and tribes can adopt more specific thresholds depending on local ecosystems (State of California, 2004; State of Oregon, 2014; State of Washington, 2012). Existing criteria have been criticized because pH levels that are known to cause biological damage fall within the allowable criteria range (Center for Biological Diversity, 2013; Weisberg et al., 2016). However, this criticism is aimed at the lower range, where OA is decreasing the pH of marine waters. On the other hand, the



upper range of allowable pH can cause both ecological harm and chemical practicalities for infrastructure. At high pH, aquatic harm can result from both ammonia increases and metal solubility/speciation changes. Similarly, high pH can cause scale buildup in pipes, damaging industrial infrastructure. Management thresholds can provide multiple functions to improve ongoing mCDR initiatives: (1) they inform the design of deployments to minimize adverse biological outcomes; (2) they guide real-time monitoring and response strategies to preserve biodiversity; and (3) their incorporation into permitting frameworks facilitates regulatory compliance and establishes industry best practices.

179 This paper focuses on identifying any mCDR-relevant carbonate chemistry threshold conditions that, if
180 exceeded, result in direct negative effects on marine species, and also on identifying any mCDR-relevant
181 carbonate chemical conditions associated with positive effects on marine species. We have considered all
182 carbonate chemistry parameters (pH, alkalinity, $p\text{CO}_2$, carbonate and bicarbonate ion concentration,
183 calcium carbonate saturation state, DIC:Alk ratio, precipitation of CaCO_3 and other minerals, etc.), though
184 only a subset is generally biologically relevant or operationally practical. We did not consider these
185 thresholds with respect to any specific mCDR method – all mCDR methods change carbonate chemistry
186 in some way and biological responses should generally be independent of how the change was generated
187 (though in the discussion we consider data suggesting this might not always be the case). We restricted our
188 consideration to just changes in carbonate chemistry and did not evaluate any of the other many potential
189 biological impacts of mCDR (Cross et al., 2023; Jewett et al., 2026; NASEM, 2022), which can be mCDR
190 method specific and may, in some cases, be much more biologically impactful than those caused by the
191 changes in carbonate chemistry (Cross et al., 2023). Although some mCDR activities may unintentionally
192 or as a by-product generate OA conditions in some regions (Cao and Caldeira, 2010), we restricted our
193 threshold evaluation to high alkalinity/low $p\text{CO}_2$ situations. While we focused on carbonate chemistry
194 parameters, discussion of some co-stressors (e.g., temperature) was unavoidable and necessary to provide
195 context or qualification. To the extent possible using existing data, we describe the taxonomic groups to
196 which thresholds may apply, what constitutes a negative biological response, the duration or temporal
197 pattern of exposure associated with the threshold and other information needed to understand the potential
198 application of a threshold. Critically, we considered the confidence or uncertainty in the thresholds with
199 regard to their application in mCDR management and make recommendations for how to improve
200 confidence (e.g., research directions, taxa to focus on).

201 In this paper, we did not attempt to characterize where, when or how organisms might be exposed to
202 conditions that exceed thresholds in the field. Similarly, we did not attempt to identify “biological



203 indicators” (i.e., species that could be monitored at a mCDR site to observe any biological impacts). Both
204 spatial mapping and identification of biological indicators can be extremely useful, but they were beyond
205 the scope of this paper.

206 **2 Methods**

207 **2.1 Literature review methods**

208 To estimate biological thresholds, we conducted a literature review to identify all studies that described
209 biological response to the carbonate chemistry conditions that could be generated by mCDR (e.g. high pH,
210 high alkalinity, etc.; BOX 2 table), regardless of the studies initial motivation. As quantified in the results
211 section, few of the studies were explicitly designed to evaluate mCDR and the majority were instead
212 focused on topics like understanding basic physiology, eco-toxicology, mitigating ocean acidification,
213 understanding biological response to natural carbonate chemistry variability, anthropogenic alkalinity
214 pollution, alkalinity enhancement in aquaculture, or other research questions. These non-mCDR studies,
215 which generally pre-date the recent emergence of mCDR research, often contain the only relevant
216 information available for certain taxa, response metrics or biological systems.

217 Literature relevant to biological thresholds for mCDR carbonate chemistry was identified by searching the
218 mCDRxFisheries Literature Database (Grabb et al., 2026), the OA-ICC biological response data portal
219 (Yang et al., 2024) with additional taxon or study-type specific searches using Google Scholar conducted
220 using search terms and filtering based on subject-matter expertise of the authors. The mCDRxFisheries
221 Literature Database is an annotated database of 870 references relevant to the intersection of mCDR,
222 fisheries and aquaculture that used a systematic approach to find and filter research articles and reports
223 that includes studies on how mCDR may affect all marine species, not just those that are fished. We used
224 the online mCDRxFisheries Literature Database Viewer
225 (<https://connect.fisheries.noaa.gov/mcdrxfisheries-lit-db-viewer/>) to search for studies that were tagged as
226 having information on any marine taxa, thresholds or biological response. The selection criteria used to
227 identify papers in the OA-ICC biological response data portal are described in the section below on OA
228 experiments relevant to mCDR.

229 To organize information on mCDR chemistry thresholds, we developed a database of information
230 extracted from studies relevant to mCDR carbonate chemistry thresholds using the lit-tag software
231 platform (McElhany et al., 2026), the same platform used for the mCDRxFisheries Literature Database.
232 The database and associated files are included as supplemental material. The online lit-tag-viewer module



233 can be used to explore the database in graphs, tables and reports
234 (<https://connect.fisheries.noaa.gov/lit-tag/>). The data collected on each study is shown in supplemental
235 material table S1-1. In our database, “study” refers to an experiment/species combination, so a single
236 published paper may include multiple studies if the paper describes the same experiment conducted on
237 multiple species or life stages or if multiple types of experiments were conducted on a single species.

238 Our review of mCDR carbonate chemistry thresholds was structured by both taxonomy and study-type.
239 We have reviewed relevant literature from physiological studies lumped into four broad taxonomic
240 groups: 1) phytoplankton and microbes, 2) macroalgae and marine plants, 3) invertebrates, including
241 zooplankton, and 4) fish. The physiological studies include experiments explicitly designed to evaluate
242 mCDR and, more commonly, that were conducted for other purposes, often for general physiological
243 insight. We have also categorized information related to thresholds based on study-type, because certain
244 types of studies may contain information on multiple taxonomic groups and the study-type itself offers
245 some unique perspectives. The study-types were divided into two broad groups: 1) OA sensitivity
246 experiments in pre-industrial conditions, and 2) field/applied studies. The field/applied studies group
247 includes: 1) mCDR pilot studies, 2) field and aquaculture OA mitigation trials, 3) parasite/pest control
248 with alkalinity, 4) waste discharge/disposal, and 5) natural analogues. The dual taxonomic/study-type
249 approach is intended to cover all the relevant data with a minimum of redundancy.

250 Some papers in non-English languages (Fan et al., 2002; Fang et al., 2000; He et al., 2017; Lin et al.,
251 2012; Liu et al., 2020; Pan et al., 2004; Pan and Jiang, 2002; Yang et al., 2004; Yao et al., 2010a; Zhang et
252 al., 2008) were explored using Artificial Intelligence (AI) tools, namely the PNNL AI Incubator’s Classic
253 Chat function (GPT-4o from OpenAI), with prompts such as “Give me the detailed experimental setup”,
254 “Give me the detailed mortality [survivability] results for all pH [alkalinity] treatments”, “Was there a
255 threshold pH [alkalinity] observed?”.

256 **2.2 Threshold methods and definitions**

257 After preliminary review of the literature, it became clear that there was limited information to describe
258 the shape of species response curves (Figure 1) with regard to mCDR carbonate chemistry. For example,
259 as captured in the database, many species response experiments were conducted at two or three pH levels,
260 which provides no data for identifying inflection points. Also, thresholds are only really clear in cases
261 where there is a tipping point type of response with a qualitative change in risk rather than cases where the
262 response is continuous (Figure 1). As a practical approach, we defined a negative threshold as the
263 chemistry level or concentration at which a study first identified a statistically significant negative



264 biological response relative to ambient control conditions. In the discussion, we relate this empirical
265 definition of a threshold to other threshold concepts like biological tipping points or management
266 thresholds. In some studies, the only data presented were for LC50 (i.e., the concentration which causes
267 the death of 50% of the study organisms). The LC50 does not provide any detail of the response curve, but
268 we assume it is likely to occur at a higher concentration than our “first detection” threshold. In our
269 database, LC50 values are categorized separately from mortality first detection thresholds. In cases where
270 no statistically significant biological response was detected after exposure to mCDR carbonate chemistry
271 conditions, we describe any potential threshold as being greater than the maximum treatment value in the
272 study. A positive maximum was identified as the level or concentration used in the study with the highest
273 statistically significant positive biological response compared to ambient control conditions. The positive
274 maximum occurs when the peak of the response curve in Figure 1a is above ambient conditions. We did
275 not attempt to identify situations where the optimum might be below ambient conditions as those would
276 be outside the range of mCDR carbonate chemistry changes. The positive maximum is not really a
277 threshold; however, it is meaningful for understanding the potential benefits of mCDR (e.g., for OA
278 mitigation) and we consider it in our analysis as a type of “threshold”. Although these thresholds are used
279 as part of the review summary, both the database and the text below provide additional information on the
280 particulars of a given study, including notes on uncertainty.

281 We considered all biological response metrics for which we found data. Information on specific response
282 metrics is retained in the database and presented in the paper text, but, for summary purposes, the response
283 thresholds were binned into general categories of mortality, sublethal effects, changes in population
284 growth, and LC50. Studies that presented results as changes in species composition (primarily
285 phytoplankton experiments) were generally considered as changes in population growth. Changes in
286 species composition could result from the direct effects of carbonate chemistry (i.e., some species have
287 lower growth rate and some higher) but may also be amplified by indirect effects of species interaction -
288 we did not attempt to parse the direct and indirect effects. We also did not attempt to calculate or
289 recalculate any carbonate chemistry parameters and relied exclusively on the parameters and units
290 presented in the original studies, with exception of converting μmol to mmol for some alkalinity
291 summaries and converting from mg L^{-1} to μmol of CaCO_3 (Rounds and Wilde, 2012). We identified the
292 carbonate chemistry equilibrium status of the exposure only if it was explicitly described in the study,
293 which, as quantified in the results section, meant that for most studies equilibrium status was “unknown”.

294 In this review, we have taken a weight-of-evidence approach to synthesizing the available data with regard
295 to mCDR thresholds rather than attempting a quantitative meta-analysis. Quantitative meta-analysis can



296 provide robust statistical tools for combining the results of multiple studies. However, it requires that the
297 studies have similar enough methodology and response metrics that it is meaningful to combine into a
298 single statistical model. Many of the studies that have information relative to mCDR thresholds would not
299 meet this criteria. We chose to consider all of the literature relevant to mCDR thresholds regardless of its
300 suitability for formal meta-analysis.

301 **3 Results**

302 The first section of the results describes the characteristics of studies compiled in the database. The
303 following sections examine the thresholds estimated for particular taxa or study types. The final section of
304 the results synthesizes the thresholds across taxa and study types.

305 **3.1 Database summary**

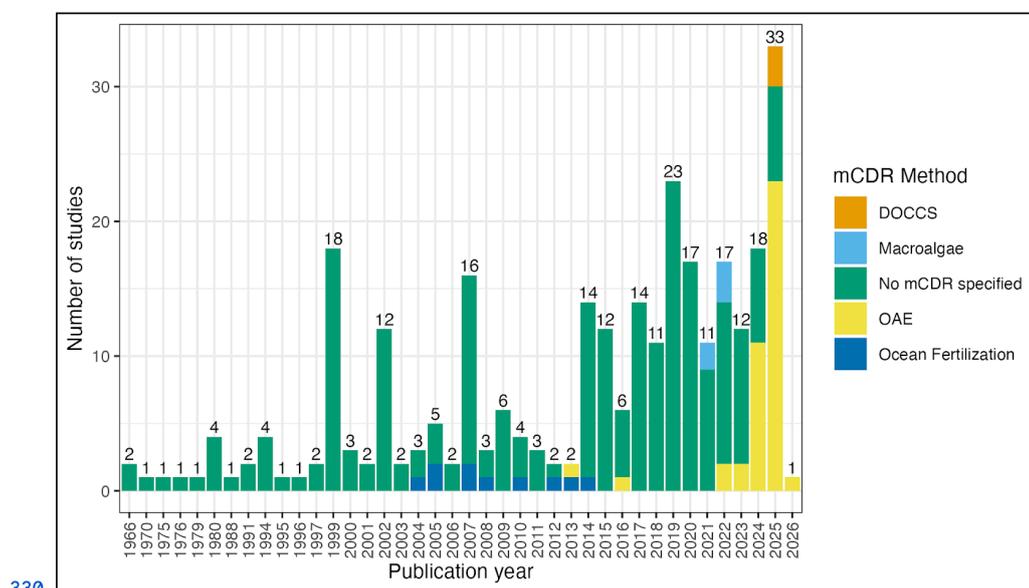
306 The database contains 310 studies, which were extracted from 194 journal articles or reports. The greatest
307 number of studies in a single paper was 10, but the majority of papers (75%) contained only a single study.
308 The database includes 256 studies (83%) from 142 papers with data that can be used to estimate either a
309 positive response, no detectable response, sublethal threshold, population growth threshold, mortality
310 threshold, or LC50 (henceforth referred to as “thresholds”). The remaining studies in the database contain
311 useful context information for considering mCDR thresholds, but are lacking quantitative threshold
312 estimates. Because an individual study can contain more than one type of threshold, the total number of
313 threshold estimates was 276.

314 Unless noted otherwise, the percentages reported in the remainder of this section refer to the number of
315 times a particular tag option occurs divided by the number of studies with a threshold ($n = 256$). Because,
316 in some cases, a study can have more than one tag option selected (e.g., a study can contain both sublethal
317 and mortality thresholds or a species can occur in both surface and mid-depths), the percentages presented
318 do not necessarily sum to 100.

319 Only a subset of the studies (17%) explicitly address mCDR with the majority of threshold information
320 extracted from studies designed for other purposes (Figure 2). Of the studies that contained thresholds,
321 78% included an expression of the threshold estimate in pH, 18% in alkalinity, 6% in $p\text{CO}_2$ and 5% as
322 “other”, which was often the concentration of chemical or feedstock added to seawater. Of the few studies
323 that expressed the threshold in more than one unit, the most common was the combination of pH and
324 alkalinity (3% of studies). A few of the threshold studies (4%) focused on mitigation for OA and an equal
325 percentage were studies focused on the addition of quicklime (CaO) for pest control. The most typical



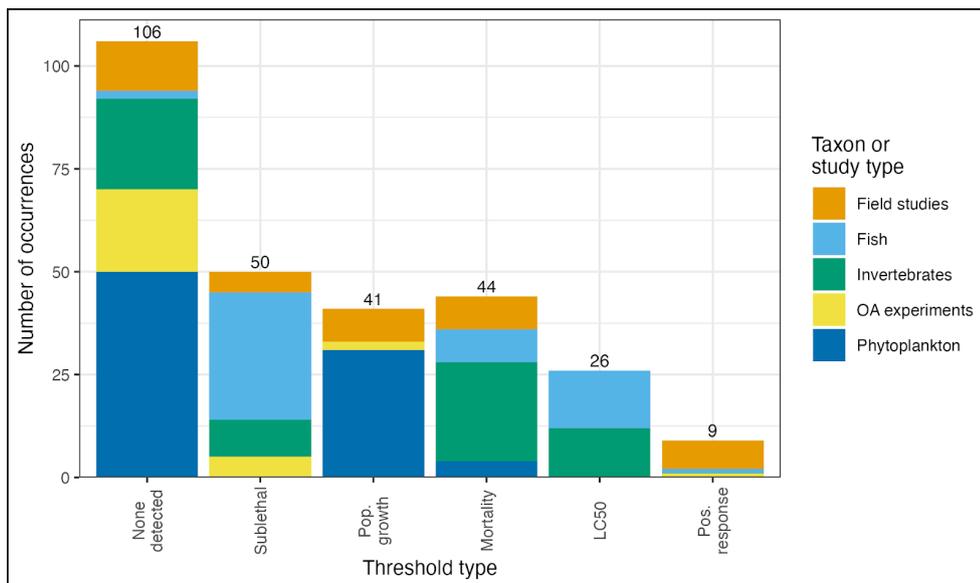
326 response was for no threshold to be detected when exposed to mCDR conditions (42% of studies), with
 327 the least common response (4%) being for a positive response (Figure 3). Pooling across all study types,
 328 the most represented taxonomic group with threshold estimates were the phytoplankton (34%), followed
 329 by invertebrates (32%), fish (21%) and finally macrophytes (5%) (Figure 4).



330

331 **Figure 2:** Study publication year and mCDR method explicitly specific in the study. The colors show the
 332 fraction of studies in each year that explicitly address specific types of mCDR.

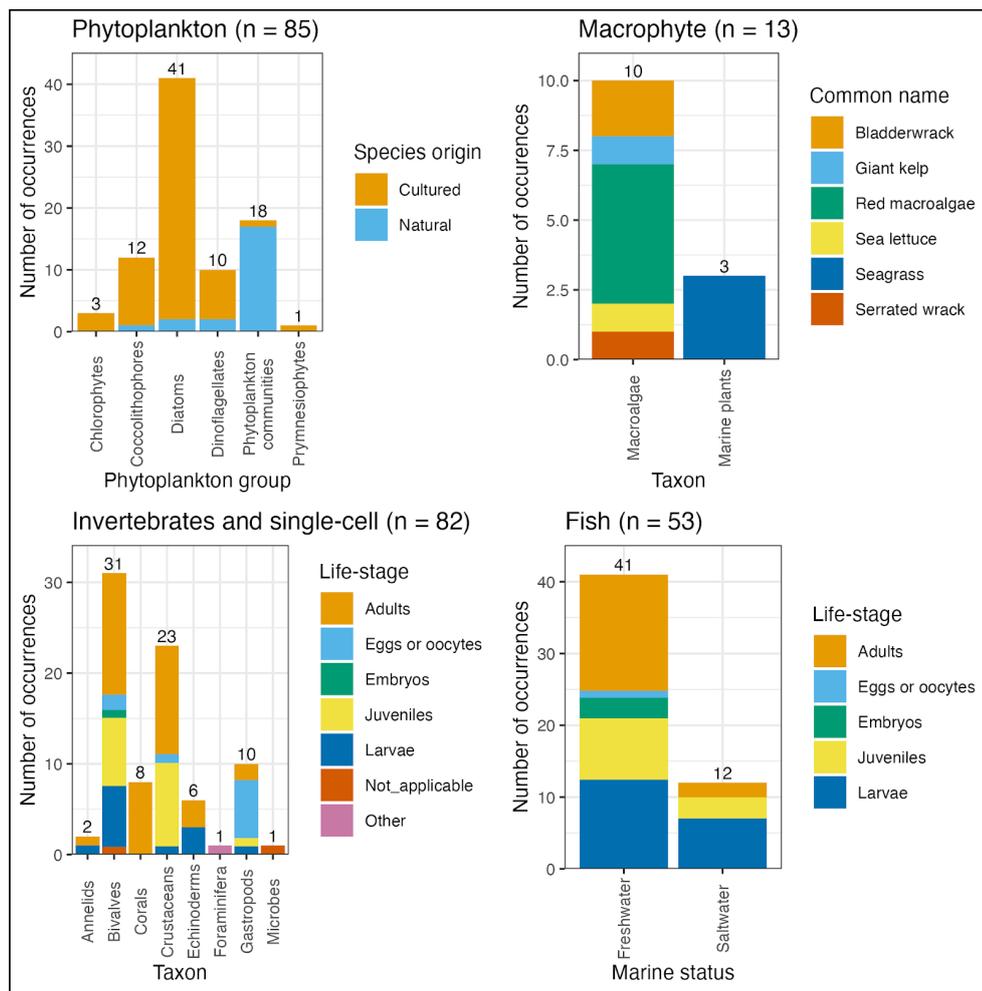
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334

335 **Figure 3:** Number of each type of threshold estimate in the database. Colors show the fraction of each
336 taxon or study type for each of the threshold types.

337



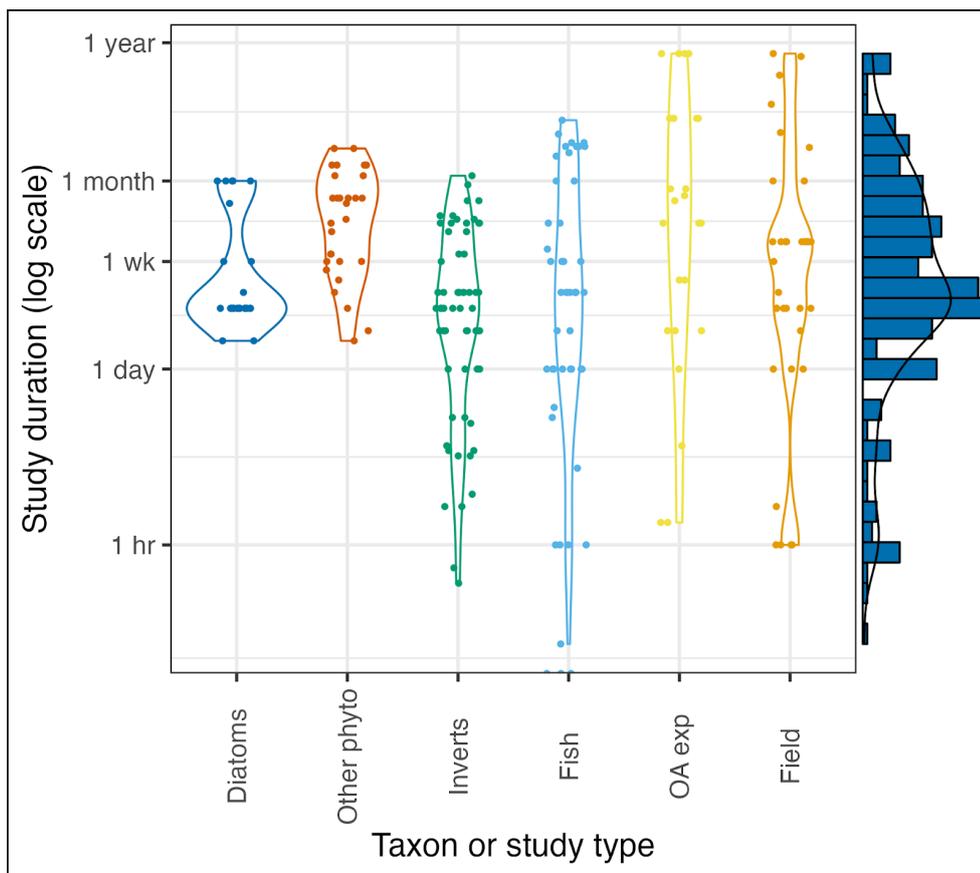
338

339 **Figure 4:** Characteristics of taxa in the database with threshold information. Data are pooled among all
 340 study types (i.e., includes OA studies and field/applied studies).

341 Most studies were relatively short with the most common duration being between a day and a week
 342 (39%), with 15% of the studies less than a day and only 6% of studies, which were all either OA
 343 experiments or field studies, lasting greater than 12 weeks (Figure 5). Many of the phytoplankton studies
 344 (29%) expressed study duration in the number of generations rather than time. The fewest number of
 345 generations was five, with most studies running for eight or fewer generations and all studies ran for 15 or
 346 fewer generations with the exception of one study that lasted 60 generations. The most common response



347 measured was “other” (35%), indicating the response metrics are very study specific. The next most
348 common metrics were mortality and population growth (Figure 6); calcification was measured in 5% of
349 the studies. Most treatment exposures (82%) were created by adding of laboratory chemicals, with 14%
350 generated by the removal of CO₂. Less common exposure methods included natural gradients and the
351 addition of mineral or effluent from mCDR pilot systems. The equilibration status of the carbonate system
352 was not explicitly stated in most of the studies (51%), with 16% of studies conducted with exposures that
353 were explicitly not in equilibrium. The majority of studies had four or fewer treatment levels, with the
354 most common number of treatment levels (24%) being only two. However, one experiment on five species
355 of diatoms had 70 treatment levels (Ferderer et al., 2025).



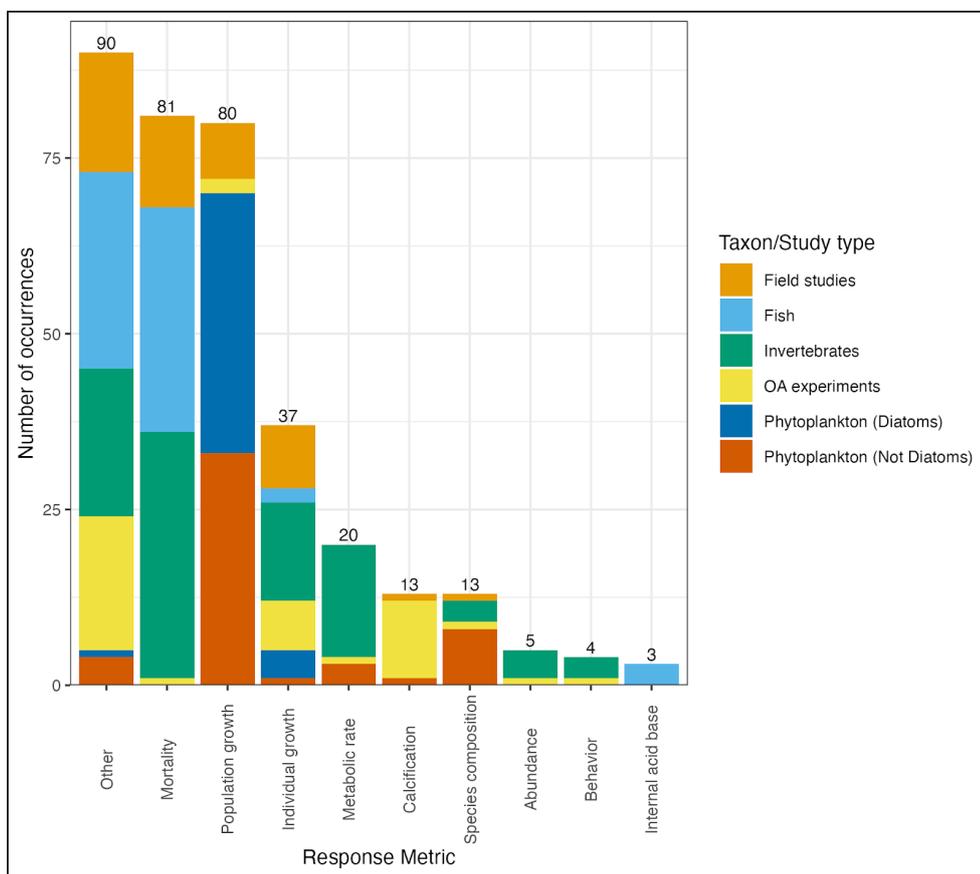
356

357 **Figure 5:** Study duration by taxon or study type for studies with threshold information. In the x-axis
358 labels, "Other phyto" refers to other phytoplankton (not diatoms), "Inverts" to invertebrates, "OA exp" to



359 OA experiments, and “Field” to field studies. The overall distribution is shown in the histogram on the
 360 right. Note that for many of the phytoplankton studies, duration was expressed in generations, not time
 361 (see text).

362



363

364 **Figure 6:** Frequency of response metrics in studies with at least one threshold. Not all metrics measured in
 365 a study were used in the estimation of thresholds.

366 The majority of studies occurred in species that inhabit the nearshore (63%) or estuary (30%). Thresholds
 367 were estimated for species directly consumed by people in 44% of the studies. Most species in the
 368 database live in benthic habitats (38%) or the surface (23%) with a few species occurring at mid-depth
 369 (2%) or the deep ocean (<1%). Calcifiers composed 42% of the threshold study species. Study species
 370 were most commonly planktonic (45%) with 31% mobile and 10% sedentary. Most species were primary



371 producers (43%) or first-order consumers (32%). The majority of study organisms (62%) were cultured as
372 opposed to originating in natural populations. The cultured organisms included laboratory phytoplankton
373 stains and species obtained from aquaculture. Species communities were evaluated in 12% of the studies
374 with the remainder focused on single species response.

375 3.2 Response studies by taxa

376 3.2.1 Phytoplankton and microbes

377 There were a total of 85 threshold estimates for phytoplankton. Because about half of the threshold
378 estimates were for diatoms ($n = 42$), summary tables and figures were separated in the categories diatoms
379 and not-diatoms. For diatoms, there were 25 no threshold detected estimates, and 17 population growth
380 thresholds. For the not-diatoms category there were four mortality threshold estimates, 25 no threshold
381 detected estimates, and 14 population growth thresholds. There were no sublethal or LC50 or positive
382 thresholds for phytoplankton. The summary table for diatom population growth thresholds (Table 2)
383 illustrates some of the data compiled in the database - the complete set of summary tables for
384 phytoplankton are included in the supplemental information (S1: tables 2a-e).

385 **Table 2:** Diatom studies in which a population growth threshold was estimated. The “Population growth
386 threshold” column shows the pH or alkalinity treatment at which population growth rate was first
387 observed to be statistically different from ambient control.



Phytoplankton (Diatoms)					
Population growth threshold					
Citation	Phytoplankton group	Species	Experiment duration	Equilibrated	Population growth threshold
Burkhardt et al. 1999	Diatoms	<i>Asterionella glacialis</i>	-	-	6 [CO ₂ ,aq] μmol kg ⁻¹
Ferderer et al. 2025	Diatoms	<i>Chaetoceros affinis</i>	3 days	No	8.49 pH
Burkhardt et al. 1999	Diatoms	<i>Coscinodiscus wailesii</i>	-	No	3–6 [CO ₂ ,aq] μmol kg ⁻¹
Søgaard et al. 2011	Diatoms	<i>Fragilariopsis nana</i>	20 days	-	9.5 pH
Ferderer et al. 2025	Diatoms	<i>Melosira sp</i>	3 days	No	8.49 pH
Scholz et al. 2014	Diatoms	<i>Nitzschia epithemoides</i>	30 days	-	8.75 pH
Bartual et al. 2002	Diatoms	<i>Phaeodactylum tricornutum clone CCAP 1052/1A</i>	4 - 6 days	No	8.5 pH
Ferderer et al. 2025	Diatoms	<i>Pseudo-nitzschia cuspidata</i>	3 days	No	8.49 pH
Burkhardt et al. 1997	Diatoms	<i>Skeletonema costatum</i>	3–4 days	No	9.03 pH
Ferderer et al. 2025	Diatoms	<i>Thalassionema nitzschioides</i>	3 days	No	8.49 pH
Chen et al. 1994	Diatoms	<i>Thalassiosira oceanica</i>	40–48 hours	Yes	8.8 pH
Oberlander et al. 2025	Diatoms	<i>Thalassiosira pseudonana Clone CCMP 1335</i>	7 days	-	8.59 pH
Chen et al. 1994	Diatoms	<i>Thalassiosira pseudonana</i>	40–48 hours	Yes	8.8 pH
Burkhardt et al. 1999	Diatoms	<i>Thalassiosira punctigera</i>	-	-	3–6 [CO ₂ ,aq] μmol kg ⁻¹
Ferderer et al. 2025	Diatoms	<i>Thalassiosira rotula</i>	3 days	No	8.49 pH
Burkhardt et al. 1999	Diatoms	<i>Thalassiosira weissflogii</i>	3 days	No	10 [CO ₂ ,aq] μmol kg ⁻¹
Li et al. 2019	Diatoms	<i>Thalassiosira weissflogii</i>	15 generations	-	8.83 pH

388

389 The recent growing interest in OAE initially raised the expectation that extensive OA-related knowledge
 390 on phytoplankton could help predict phytoplankton responses under OAE conditions, which alter seawater
 391 pH in the opposite direction to OA. Over the past five years, experimental OAE research has focused on
 392 abrupt exposure to alkalization under air-equilibrated (see Box 2 for discussion of equilibration) and
 393 non-equilibrated conditions, using cultures, microcosm or mesocosm experiments and deck incubations,
 394 monitored typically over days or weeks, spanning a few generations. These experiments offer a snapshot
 395 of the short and medium-term physiological and community-level responses to elevated pH and/or the



396 associated changes in carbonate chemistry caused by alkalinity, rather than insight into steady state or
397 transgenerational adaptation away from the point of deployment (Renforth and Henderson, 2017).

398 In these studies, two main experimental approaches have been adopted. Some experiments applied
399 moderate increases in TA and, consequently, in pH (e.g., (Guo et al., 2025; Hutchins et al., 2023). In other
400 cases, higher levels of alkalinity were applied, as suggested by the OAE best practice guide
401 (Iglesias-Rodríguez et al., 2023), in order to explore environmental safety threshold alkalinity levels (e.g.,
402 Delacroix et al., 2024) and mimicking carbonate chemistry conditions at the site of deployment (e.g.,
403 Gately et al. 2023).

404 When the perturbation applied was mild (e.g., increase in Δ TA between 16-29 $\mu\text{mol kg seawater}^{-1}$, (e.g.,
405 Hutchins *et al.* 2023; Guo *et al.* 2025), resulting in only minor alterations in pH and carbonate system
406 chemistry, OAE did not cause significant changes in either the overall planktonic community (Guo et al.,
407 2025) or in individual algal species (Delacroix et al., 2024). Notably, the primary objective of these
408 experiments was to evaluate and compare different materials (e.g. alkalinity released by industrial
409 by-products like lime or steel slag, or silicate rocks etc.) and methodological approaches (e.g. adding
410 alkaline solutions such as NaOH), utilizing electrochemical processes, spreading finely ground alkaline
411 particles over the open ocean). Both studies ultimately demonstrated that any observed negative impacts
412 on planktonic communities or on specific organisms were attributable to the release of chemical
413 compounds from the tested materials (e.g., $\text{Ca}(\text{OH})_2$, olivine, steel slag), rather than to the magnitude of
414 alkalinity enhancement itself.

415 Other experiments were designed using values based on model-predicted OAE scenarios that provide
416 estimated seawater carbonate chemistry conditions assuming extensive global alkalinity addition
417 (Renforth and Henderson 2017). Those studies focus on moderate-to-severe localized effects on ocean
418 chemistry (e.g. Xin et al., 2024). In the experiments presented in these studies, alkalinity was added to
419 achieve a TA of up to 3000 $\mu\text{mol kg seawater}^{-1}$ and/or pH values with a typical upper limit of ~ 8.6 , and
420 higher alkalinities led to secondary precipitation, resulting in alkalinity loss (Paul et al., 2025). Under
421 these conditions, results indicate variable physiological and biogeochemical changes in phytoplankton,
422 including neutral effects (Gately et al., 2023; Marín-Samper et al., 2024). Observed functional changes
423 include a 30% decline in primary production in a North Atlantic central gyre, shifts toward smaller cell
424 sizes (Subhas et al., 2022), shifts in bacteria production (Ferderer et al., 2022), and diatom selection as a
425 function of the type of alkalinity (i.e., greater silicification rates under silicate-based mineral treatment
426 (Ferderer et al., 2024).



427 In a culture experiment with the coccolithophore *Emiliana huxleyi* exposed to elevated alkalinity under
428 non-equilibrated conditions, a threshold for growth was identified at $\Delta\text{TA} \sim 600 \mu\text{mol kg}^{-1}$, linked to CO_2
429 limitation, even though the PIC:POC ratio remained stable. The authors suggest a threshold value for
430 growth at $f\text{CO}_2$ of 110, corresponding to a pH of 8.6 (Faucher et al., 2025). Building on this, Kousoulas et
431 al. (2025) directly tested how pH changes induced by NaOH addition influence plankton communities. In
432 their experiment, an abrupt overshoot in pH (to 8.6–8.7), beyond typical natural variability, delayed the
433 onset of a diatom bloom and caused moderate shifts in species composition. Because even small changes
434 in community structure or function can have ripple effects on ecosystems (Dutkiewicz et al., 2021), these
435 apparently modest physiological changes and shifts in % contribution of function warrant further
436 exploration.

437 Given the widespread presence of carbon concentrating mechanisms (e.g., carbonic anhydrase, ionic
438 pumps) in phytoplankton, most studies have focused on whether increased alkalization could impact
439 photosynthesis and induce biotic or abiotic calcification. While biotic calcification appears to be mostly
440 unaffected, abiotic precipitation and nutrient removal from solution were observed under TA values above
441 $3000 \mu\text{mol kg seawater}^{-1}$ (Gately et al., 2023).

442 3.2.2 Macrophytes

443 All the studies that estimate thresholds for macrophytes (macroalgae and marine plants) are included in
444 the OA experiment and field/applied sections. Although macrophyte data are included in the threshold
445 summary tables associated with those sections of the paper, we here provide background information
446 related to threshold for these taxa.

447 Macroalgae occupy a global surface area of 6.06–7.22 million km^2 and a net primary productivity (NPP)
448 of 1.32 Pg C/year (Duarte et al., 2022). Ongoing research on the CDR potential of macroalgae has
449 explored the fate of macroalgal carbon before, during and after decomposition to include vertical and
450 horizontal transport of macroalgal carbon, export, burial and carbon losses as particulate carbon or
451 dissolved carbon through the water column (Dolliver and O'Connor, 2022). Macroalgae are particularly
452 interesting because their decomposition does not only release CO_2 , but also produces comparable amounts
453 of bicarbonate ions, thus raising seawater alkalinity and enhancing carbon sequestration (Lee et al., 2025;
454 Xiong et al., 2023). Therefore, their role in global NPP and their natural ocean alkalinity enhancement
455 during decomposition as well as their production of recalcitrant DOC (the fraction of DOC that is resistant
456 to rapid microbial degradation) makes macroalgae good candidates for blue carbon programs and mCDR
457 (Krause-Jensen and Duarte, 2016; Lee et al., 2025). However, one question remains – how will



458 macroalgae respond to alterations in chemistry driven by mCDR approaches such as OAE or other
459 electrochemical manipulations of seawater to determine if their physiological performance and fluxes of
460 CO_2 , HCO_3^- and DOC are maintained.

461 Data regarding the effect of elevated pH or alkalinity on the physiological performance of macroalgae are
462 scarce. We know that macroalgal habitats experience high fluctuations in pH, particularly in coastal
463 systems, experiencing pH values as high as 10 (Björk et al., 2004; Menéndez et al., 2001a). In addition,
464 macroalgae possess efficient carbon concentrating mechanisms that enable them to utilize bicarbonate
465 ions, in addition to CO_2 , under conditions of elevated pH (Raven et al., 2012; Sun et al., 2023).
466 Experiments on the role of seasonal and diurnal variability in pH and DIC in three species of ecologically
467 important shallow-water macroalgae (*Fucus vesiculosus*, *F. serratus*, *Ceramium rubrum* and *Ulva* sp.)
468 revealed that photosynthesis in these species was not limited by natural concentrations of inorganic carbon
469 (Middelboe and Hansen 2007). The study by Middelboe and Hansen (2007) found that maximum
470 photosynthesis and inorganic carbon concentrations at saturation were lower when measured at pH 9.3
471 than at pH 8 and do not rely on CO_2 , which can be limiting at elevated pH. They also found that some
472 species, such as *F. serratus*, can acclimate their photosynthetic carbon fixation to elevated pH. The authors
473 suggest, however, that high pH may have a direct effect on macroalgal physiology apart from the influence
474 of inorganic carbon. Indeed, macroalgae and most marine photosynthetic organisms are not limited by
475 dissolved inorganic carbon; however membrane transport processes and metabolic functions involved in
476 internal pH regulation may be affected by alkalization (Middelboe and Hansen, 2007). Also, shifts in the
477 cellular abundance and composition of amino acids driven by alkalization might affect cellular growth
478 (Taraldsvik and Mykkestad, 2000).

479 3.3.3 Invertebrates, including zooplankton

480 There are a total of 67 threshold estimates for invertebrates. For invertebrates, there are 12 LC50
481 estimates, 24 mortality threshold estimates, 22 no threshold detected values, and 9 sublethal thresholds.
482 There are no population growth or positive thresholds for invertebrates. The summary table for LC50
483 estimates (Table 3) illustrates some of the data compiled in the database - the complete set of summary
484 tables for invertebrates are included in the supplemental information (S1: tables 3a-d).

485 **Table 3:** Invertebrate studies in which LC50 was estimated.



Invertebrates					
LC50					
Citation	Taxon	Species	Life stage	Experiment duration	LC50
Maoxiao et al. 2018	Bivalves	Chinese razor clam (<i>Sinonovacula constricta</i>)	Juveniles	48 hours	9.86 pH at 48h
Hansen et al. 2017	Crustacean	Copepod (<i>Acartia spp</i>)	Adult; eggs or oocytes; nauplii	48-72 hours	8.72 pH at 72h; 9.03 pH at 48h
Hansen et al. 2017	Crustacean	Copepod (<i>Centropages typicus</i>)	Adult; eggs or oocytes; nauplii	48-72 hours	8.90 pH at 72h; 9.31 pH at 48h
Hansen et al. 2017	Crustacean	Copepod (<i>Eurytemora affinis</i>)	Adult; eggs or oocytes; nauplii	48-72 hours	9.51 pH at 72h
Hansen et al. 2017	Crustacean	Copepod (<i>Oithona similis</i>)	Adult	72 hours	8.39 pH at 72h; 8.6 pH at 48h; 8.74 pH at 24h
Hansen et al. 2017	Crustacean	Copepod (<i>Pseudocalanus elongatus</i>)	Adult	72 hours	9.24 pH at 72h; 9.65 pH at 48h
Hansen et al. 2017	Crustacean	Copepod (<i>Temora longicornis</i>)	Adult	72 hours	8.44 pH at 72h; 8.83 pH at 48h
Locke et al. 2009	Crustacean	Sand shrimp (<i>Crangon septemspinosus</i>)	Adult	96 hours	9.70 pH at 96h
Locke et al. 2009	Crustacean	Sand shrimp (<i>Crangon septemspinosus</i>)	Adult	14 days	9.20 pH at 14d
Yang et al. 2004	Crustacean	Whiteleg shrimp (<i>Penaeus vannamei</i>)	Juveniles	96 hours	12000 µmol/L
Yao et al. 2010	Crustacean	Whiteleg shrimp (<i>Penaeus vannamei</i>)	Juveniles	48 hours	36.81mmol·L ⁻¹ at pH 8.8; 33.05 mmol·L ⁻¹ at 9.2; 5.55 mmol·L ⁻¹ at 9.6
Jones et al. 2025	Gastropod	Taylor's sea hare (<i>Phyllaplysia taylori</i>)	Adult	96 hours	8.3 pH at 72h; 9.3 at 12h

486

487 Various phyla of marine invertebrates include calcifying species, meaning these animals produce calcium
 488 carbonate minerals (e.g., calcite, aragonite) to form their shells, endoskeletons, or exoskeletons. Namely,
 489 these invertebrate groups are the arthropods, brachiopods, bryozoans, cnidarians (corals, hydrozoans),
 490 echinoderms, mollusks, and sponges (calcareans). Many of these organisms have ecological, cultural,
 491 and/or economic significance (e.g., bivalves, corals, crustaceans). Very few studies so far have
 492 investigated the potential effects of OAE and other mCDR approaches on the growth and survival of
 493 invertebrate species (e.g., copepods [(Bhaumik et al., 2025; Camatti et al., 2024; Kousoulas et al., 2025;
 494 Nocera et al., 2025)], crabs [(Cripps et al., 2013)], isopods [Jones *et al.* 2025], gastropods [Jones *et al.*
 495 2025]). Nonetheless, various laboratory experiments with elevated pH and/or alkalinity have been carried
 496 out in the context of aquaculture, biofouling management, or fundamental research, some of them dating
 497 back to the 1960s, and this work could help establish mCDR thresholds. These experiments on
 498 invertebrates were conducted on both planktonic species or life stages (i.e., pelagic larvae) and benthic
 499 species (juvenile and adult life stages). Taxa included bivalves, gastropods, crustaceans, and echinoderms,



500 as well as broad zooplankton communities. These experiments varied greatly in duration (from 15 min to
501 100 days), maximum pH exposure (most often 9.5 but up to 12.7), and response variables (e.g., mortality,
502 behavior, metabolic rates).

503 Among crustaceans, various shrimp species and life stages (i.e., larvae, juveniles, and adults) seemed
504 unaffected by pH up to 9.5 for short periods of time (i.e., 24-96 h), but only up to pH around 8.5 for longer
505 durations (14 days), with mortality increasing to 100% at higher pH levels (up to 12.6) (Fang et al., 2000;
506 Huang et al., 2020; Locke et al., 2009; Wang et al., 2002; Yang et al., 2004; Yao et al., 2010a; Zhang et al.,
507 2008). For adult amphipods, mortality rates depended on the exposure duration: the longer the exposure,
508 the lower the pH leading to 50% mortality (i.e., 8.7 for 96 h exposure, 9.9 for 24 h exposure) (Xue et al.,
509 2020). While adult eelgrass isopods (*Idotea resecata*) experienced some mortality between pH 7.8 and 9.3
510 after 96 h exposure, levels never reached 50% mortality (Jones et al., 2025). Copepods' sensitivity to pH
511 varied between species and life stages (from eggs to adults), especially depending on whether they were
512 more oceanic (higher sensitivity) or estuarine (lower sensitivity), with greater mortality at pH between 8.4
513 and 9.5 after 72 h exposure (Bhaumik et al., 2025; Camatti et al., 2024; Gim et al., 2018; Hansen et al.,
514 2017). No similar experiments have been conducted on crabs or lobsters to date, although a study on adult
515 European green crabs (*Carcinus maenas*) found no detectable metabolic response at pH up to 8.77 (Cripps
516 et al., 2013).

517 Among mollusks, studies on bivalves mostly focused on adults, though eggs, embryos, larvae, and
518 juveniles were also considered, while studies on gastropods largely focused on eggs, with a couple more
519 on larvae and adults; no experiments were conducted on the other classes of mollusk. Because of adult
520 bivalves' ability to close off their valves, they seemed less sensitive to elevated pH than larvae. Mortality
521 of clam and oyster eggs, embryos, and larvae significantly increased above pH 8.5 (Calabrese, 1970;
522 Calabrese and Davis, 1966; Huo et al., 2019). Juvenile Chinese razor clams (*Simonovacula constricta*) did
523 not experience increased mortality until pH 9.2 (Maoxiao et al., 2018), but juvenile Japanese geoducks
524 (*Panopea japonica*) did experience increased mortality at pH 8.4 (Huo et al., 2019). As for adults, while
525 Chinese clams (*Cyclina sinensis*) experienced increased mortality at pH 9, no threshold could be detected
526 for the other species with maximum pH exposure ranging from 8.2 to 12.7 (Comeau et al., 2017; Fan et
527 al., 2002; He et al., 2017; Lin et al., 2012; Liu et al., 2020; Shumway et al., 1988a). In gastropods, none of
528 the experiments on eggs or larvae of various limpet species resulted in detectable mortality thresholds,
529 with pH exposure up to 10.2, although none of the experiments lasted more than 24 h (Aquino De Souza
530 et al., 2009; Cañizares et al., 2022; Castejón et al., 2021; Guallart et al., 2020). Adult Taylor's sea hares
531 (*Phyllaplysia taylori*), which do not have an external shell seem to have expressed more sensitivity than



532 bivalves, showing over 50% mortality at pH 8.3 and 100% at pH 9.3 after 96 h exposure (Jones et al.,
533 2025).

534 Only two laboratory experiments focused on echinoderms (both sea urchins), neither of which detected a
535 mortality threshold under pH exposure up to 8.3 (Gim et al., 2018; Mos et al., 2020).

536 In summary, the experiments to date on the effects of elevated pH or alkalinity on invertebrates display a
537 large variation in species and life stage response to conditions potentially similar to those obtained with
538 OAE manipulations. Compared to the large diversity of calcifying invertebrates, this review highlights a
539 poor taxonomic coverage, with limited studies on echinoderms and a total lack of relevant experiments on
540 corals, hydrozoans, bryozoans, brachiopods, and calcareous sponges.

541 3.3.4 Fish

542 There are a total of 56 threshold estimates for fish. For fish, there are 14 LC50 estimates, eight mortality
543 threshold estimates, two no threshold detected values, one positive threshold and 31 sublethal thresholds.
544 There are no population growth thresholds for fish. The summary table for mortality thresholds (Table 4)
545 illustrates some of the data compiled in the database - the complete set of summary tables for fish are
546 included in the supplemental information (S1: tables 4a-e).

547 **Table 4:** Fish studies in which a mortality threshold was estimated. The “Mortality threshold” column
548 shows the pH or alkalinity treatment at which mortality was first observed to be statistically different from
549 ambient control.



Fish					
Mortality threshold					
Citation	Fresh or salt water	Species	Life stage	Experiment duration	Mortality threshold
Daye et al. 1980	Freshwater	Atlantic salmon (<i>Salmo salar</i>)	Embryos; larvae	3 months	9.5 pH
Foldvik et al. 2022	Freshwater	Atlantic salmon (<i>Salmo salar</i>)	Embryos	5 - 1180 minutes	12.23 pH
Daye et al. 1975	Freshwater	Brook trout (<i>Salvelinus fontinalis</i>)	Larvae	1 weeks	9.8 pH
Yao et al. 2010	Freshwater	Medaka (<i>Oryzias latipes</i>)	Embryos; larvae	70 days	16500 µmol/L
Wagner et al. 1997	Freshwater	Rainbow trout (<i>Oncorhynchus mykiss</i>)	Adult	24 hours	9.3 pH
Witschi et al. 1979	Freshwater	Rainbow trout (<i>Oncorhynchus mykiss</i>)	Juveniles	48 hours	9.0
Kong et al. 2023	Saltwater	Obscure puffer (<i>Takifugu obscurus</i>)	Eggs or oocytes	210 hours	9.5 pH
Harper et al. 2014	Saltwater	White sucker (<i>Catostomus commersoni</i>)	Larvae	96 hours	78580 µmol/L

550

551 Our literature review identified experimental studies examining the impacts of elevated pH and alkalinity
 552 across 30 species, yielding data from 49 unique experimental exposures. Of the species tested, 22 were
 553 freshwater taxa, and only eight were marine or euryhaline fish tested under brackish or fully saline
 554 conditions. As discussed below, freshwater fish are likely to differ from saltwater fish in their response to
 555 elevated pH or alkalinity. However, freshwater fish are included in our summary because they may
 556 provide some insight into the sensitivity of marine species, albeit with substantial caveats. With respect to
 557 life stage, 29 exposures focused on juveniles or adults, while the remaining 20 examined embryos or
 558 larval stages (Fig. 4). Across 22 studies spanning 18 species, we identified a survival threshold, reported
 559 either as a LC50 or as the lowest pH/alkalinity treatment that produced significantly higher mortality than
 560 the control. In addition, 28 studies spanning 17 species did not examine lethal effects but reported a
 561 sublethal threshold, where at least one biological function was negatively affected by elevated
 562 pH/alkalinity. Only two studies found no effect at the levels tested. Importantly, only one study explicitly
 563 evaluated the impacts of OAE. Whereas all other studies were motivated by natural or anthropogenic
 564 alkalinization in freshwater systems, or to better understand the effects of elevated pH and alkalinity in
 565 aquaculture settings. This context shaped key aspects of experimental design, including treatment levels,
 566 alkalinity feedstocks, and the response traits assessed.

567 The OA literature suggests that fish early life stages exhibit the strongest physiological responses to
 568 altered pH and carbonate chemistry (Baumann, 2019). This pattern may also apply to OAE and other
 569 high-pH scenarios, yet, empirical evidence for early-life responses to elevated pH/alkalinity remains



570 limited, particularly in marine species. Two studies in our database reported 24-hour LC50 values for
571 survival in five marine fish larvae (Table 4). Brownell (1980) reported LC50 values in newly hatched
572 larvae of pH 8.67 for Cape rockling (*Gaidropsarus capensis*), pH 8.78 for Cape sole (*Heteromycteris*
573 *capensis*), and 8.82 for common white seabream (*Diplodus sargus*) (Brownell, 1980). Gilthead seabream
574 (*Sparus aurata*) showed LC50s of pH 8.66, 9.26, and 8.75 at 12, 20, and 52 days post-hatch respectively,
575 whereas Senegalese sole (*Solea senegalensis*) showed LC50s of pH 8.94, 9.57, and 9.40 at 7, 20, and 32
576 days post-hatch respectively (Parra and Yúfera, 2002). The only other survival data on marine fish larvae
577 come from a large mesocosm study that tested the impacts of OAE on Atlantic herring (*Clupea harengus*)
578 larvae, which reported no effects on mortality or growth rates during a two week exposure to pH levels up
579 to 8.7 (Goldenberg et al., 2024).

580 Three other studies reported juvenile mortality thresholds in marine or euryhaline taxa. Juvenile spotted
581 scat (*Scatophagus argus*), a tropical to subtropical euryhaline fish, exhibited 24-, 48-, and 96-hour LC50s
582 of 50,540, 33,020, and 29,590 $\mu\text{mol L}^{-1}$ TA, values that are over ten times greater than typical marine TA
583 (Kong et al., 2025). Juvenile turbot (*Scophthalmus maximus*) showed indications of stress response at pH
584 above 8.3, showing increased frequency of nuclear anomalies and reduced alkaline phosphatase activity
585 (Wang et al., 2019). In the euryhaline sheepshead minnow (*Cyprinodon variegatus*), exposure up to pH
586 8.45 for 96 hours had no effect on short-term survival; the age and developmental stage of these test fish
587 was not reported (Gim et al., 2018).

588 Early-life responses to elevated pH/alkalinity are better documented for freshwater fish. Harper et al
589 (2014) examined the impacts of elevated alkalinity in seven North American freshwater species
590 potentially affected by river alkalization and found a wide range of 96-hour LC50 values following
591 dosing with sodium bicarbonate (NaHCO_3). The lowest LC50s (highest sensitivity) were observed in pallid
592 sturgeon (*Scaphirhynchus albus*; 12,160 $\mu\text{mol L}^{-1}$ TA), shovelnose sturgeon (*Scaphirhynchus*
593 *platyrhynchus*; 17,600 $\mu\text{mol L}^{-1}$ TA), and fathead minnow (*Pimephales promelas*; 21,780 $\mu\text{mol L}^{-1}$ TA),
594 whereas walleye (*Sander vitreus*; 40,404 $\mu\text{mol L}^{-1}$ TA), white sucker (*Catostomus commersonii*; 53,360
595 $\mu\text{mol L}^{-1}$ TA), northern pike (*Esox lucius*; 83,620 $\mu\text{mol L}^{-1}$ TA), and rainbow trout (102,680 $\mu\text{mol L}^{-1}$ TA)
596 were more tolerant (Harper et al., 2014). Another study focused on fathead minnow found a higher
597 72-hour LC50 at 67,860 $\mu\text{mol L}^{-1}$ TA (Elskus et al., 2015). A study that exposed medaka (*Oryzias latipes*)
598 to a range of alkalinity levels, found embryo survival declined significantly at 16,500 $\mu\text{mol L}^{-1}$ TA, while
599 larval growth rate was reduced at 5,300 $\mu\text{mol L}^{-1}$ TA (Yao et al., 2010b).

600 Several studies focused on impacts of alkalization on the early-life survival of Salmonids. In Atlantic
601 salmon (*Salmo salar*), embryos showed no changes in survival or developmental rate at pH 9.0 and 9.5



602 relative to a control group (pH 6.8); however, after hatching, larvae at the highest pH (9.5) exhibited an
603 18% increase in mortality, along with histological indicators of cellular damage emerging at pH 9.0 (Daye
604 and Garside, 1980). Another study confirmed that Atlantic salmon embryos can tolerate levels up to pH
605 11.34, but reported complete mortality at pH 12.23 (Foldvik et al., 2022). Fingerling brook trout
606 (*Salvelinus fontinalis*) exposed for a week to a gradient of pH levels showed increased mortality at pH 9.8
607 (Daye and Garside, 1975) along with cellular damage in gill and operculum tissue beginning at pH 9.0
608 (Daye and Garside, 1976). Juvenile rainbow trout (*Oncorhynchus mykiss*) showed a 30% reduction to
609 survival after 24-hours exposure to pH 9.5, and complete mortality at pH 10.0 (Witschi and Ziebell, 1979).
610 In another survey focused on rainbow trout, hatchery-reared juveniles that were transplanted to field
611 environments with differing pH conditions showed that groups exposed to pH > 9.3 showed large
612 reductions in survival after 96 hours (Wagner et al., 1997).

613 Sub-lethal impacts of elevated pH and/or alkalinity were reported in 25 studies covering 31 species of
614 freshwater and marine fish (Table S1-4ca). The types of sublethal traits measured were highly varied but
615 included histological changes, shifts in plasma ion concentrations, alterations in gene expression, enzyme
616 activity and stress hormone levels, and changes in ammonia excretion. The study by Brownell (1980)
617 reported 24-hour EC50 values for inhibition of first-feeding, a key trait for larval survival, at pH 8.67 for
618 Cape rockling, pH 8.78 for Cape sole, and pH 8.82 for common white seabream. These results indicate
619 that sublethal impacts occur at pH levels approximately 0.3-0.6 units lower than the estimated LC50 for
620 larval survival in these species (Brownell 1980). Several studies on freshwater taxa have examined the
621 effects of elevated pH on ammonia excretion, finding that pH 9.5 can effectively block gill ammonia
622 efflux, leading to accumulation in muscle tissue, which is a stressful condition that may become lethal
623 over time (Laurent et al., 2000; Scott et al., 2005; Scott and Wilson, 2007; Wilkie and Wood, 1991, 1994,
624 1995). However, these studies generally tested only a single elevated pH treatment, so the true threshold
625 for this response has not been evaluated.

626 Freshwater and marine species exhibit important differences in ion- and osmoregulatory mechanisms due
627 to the contrasting osmotic pressures of their respective environments (Kültz and Gilmour, 2020).
628 Consequently, general sensitivity to elevated pH and alkalinity is expected to differ between freshwater
629 and marine taxa. Furthermore, differences in how pH responds to alkalinity additions in freshwater versus
630 seawater complicates how the results reported here can be extrapolated to OAE sensitivity of marine fish.
631 Many of the freshwater studies in our database used NaHCO₃, which increases total alkalinity and
632 dissolved inorganic carbon together and usually produces modest pH changes unless CO₂ exchange is also
633 involved (Dickson, 2010). In contrast, many OAE approaches involve adding strong base (e.g., NaOH) or



634 other alkaline materials, which can raise pH more sharply for a given alkalinity addition prior to
 635 equilibration with atmospheric CO₂. Thus, these studies provide important baseline information on fish
 636 tolerance but highlight major knowledge gaps in how marine taxa will respond to elevated pH and
 637 alkalinity under OAE.

638 3.4 Evaluation by study-type

639 3.4.1 Ocean acidification sensitivity experiments

640 There are a total of 28 threshold estimates from OA experiments. There are 20 no threshold detected
 641 values, 2 population growth thresholds, 1 positive threshold and 5 sublethal thresholds. There are no LC50
 642 or mortality thresholds for the OA experiments. The summary table for OA experiment sublethal
 643 thresholds (Table 5) illustrates some of the data compiled in the database - the complete set of summary
 644 tables for fish are included in the supplemental information (S1: tables 5a-d).

645 **Table 5:** OA experiment studies in which a sublethal threshold was estimated. The “Sublethal threshold”
 646 column shows the pH or alkalinity treatment at which a sublethal effect was first observed to be
 647 statistically different from ambient control. A sublethal effect was any negative biological change that did
 648 not result in death during the experiment.

OA experiments					
Sublethal threshold					
Citation	Taxon	Species	Life stage	Experiment duration	Sublethal threshold
Waldbusser et al. 2016	Bivalves	Olympia oyster (<i>Ostrea lurida</i>)	Larvae	5 days	4 Ω _{arg}
Pajusalu et al. 2016	Macroalgae	Red macroalgae (<i>Furcellaria lumbricalis</i>)	Adult	1 days	8.94 pH
Miller et al. 2017	Marine_plant	Sea grass (<i>Zostera japonica</i>)	Adult	1.5 hours	8.4 pH
Zhang et al. 2018	Phytoplankton	Coccolithophore (<i>Emiliana huxleyi</i>)	Not_applicable	7 generations	8.45 pH
Torstensson et al. 2015	Phytoplankton	Diatom (<i>Nitzschia lecontei</i>)	Not_applicable	60 generations	280 μatm

650 The field of OA research is a foundation for understanding how changes in seawater pH affect marine
 651 ecosystems, offering decades of experimental, observational, and modeling insights into organismal and
 652 ecological responses (Doney et al., 2020; Martins Medeiros and Souza, 2023; Sundin, 2022). A subset of
 653 the OA species-response experiments simulated not only projected future, lower pH conditions relative to
 654 present-day, but also included pre-industrial, high pH, treatments, often created by bubbling seawater with



655 low pCO₂ air to raise pH relative to ambient conditions. Experimental guidelines recommended that a
656 baseline control treatment for which to compare future atmospheric CO₂ levels would be a “preindustrial”
657 climate near 280 ppm pCO₂ atm since it represents long-term (millennial) average concentration that
658 shaped species performance and ecosystem function (Barry et al., 2010). This experimental approach
659 closely parallels decarbonization of seawater via DOCCS (Direct Ocean Carbon Capture and Storage), in
660 which inorganic carbon is extracted from seawater and seawater returned to the ocean is depleted in
661 dissolved CO₂ compared to surrounding waters, thereby elevating pH locally and enhancing the gradient
662 that drives air-sea CO₂ uptake.

663 We relied on the publicly-available Ocean Acidification International Coordination Center (OA-ICC)
664 Biological Response Data Portal, which has OA datasets in standardized, accessible formats
665 (<https://www.iaea.org/services/oa-icc>), to identify peer-reviewed studies that included low pCO₂ (high pH)
666 treatments. We identified 16 studies with “pre-industrial” treatments achieved by modifying DIC (as
667 opposed to alkalinity modification). The range of taxa studied were diverse, including primary producers -
668 macroalgae, seagrass, and phytoplankton - to primary consumers - echinoderms, bivalves, corals, and
669 foraminifera. The response metrics for primary consumers included primary production rates and
670 population growth rates, while the response metrics for primary consumers ranged from shell and skeletal
671 metrics to developmental metrics. Two studies measured community-level responses: one on benthic
672 foraminiferal diversity and the other on net community calcification in rocky intertidal pools. Within
673 studies, the maximum pH tested ranged from 8.06 to 10.25, with maximum pH tested for most studies in
674 the 8.3-8.5 range. Mostly, there were no effects of elevating pH beyond present-day conditions (e.g., from
675 8.0 to 8.3). However, the exceptions to detecting thresholds were for some of the primary producers
676 studied. There were negative effects of elevating pH (by reducing DIC) for sublethal and/or
677 population-level response metrics in seagrass, coccolithophores, and red macroalgae. For seagrass, of two
678 *Zostera* spp. studied (*Z. marina* and *Z. japonica*), only *Z. japonica* exhibited sensitivity to increased pH
679 (Miller et al. 2017). In this species, maximum photosynthetic rate (P_{max}) linearly declined from pH 8.0 to
680 8.2 and up to 8.4. At 8.4, P_{max} was 50% of that measured at 8.0. Similarly, the red macroalga, *Furcellaria*
681 *lumbricalis*, exhibited a 20% decline in net photosynthetic rate between pH 8.94 relative to 7.98 during an
682 un-replicated field mesocosm experiment (Pajusalu et al., 2016). However, the robustness of this observed
683 effect is challenged in that it was only observed in one of two years in which experiments were conducted.
684 Another study that measured primary production metrics in three red macroalgae (*Heminuera frondosa*;
685 *Rhodymeia* sp.; *Plocamium angustum*) observed no effect of a high pH treatment relative to present-day
686 pH (Cornwall and Hurd, 2019). However, the change in pH among these two treatments was minimal,
687 from 8.12 to 8.15.



688 Among these OA studies, there was one which implemented a different experimental design than typically
689 utilized by OA studies (i.e., with best practices emphasizing replication over the number of treatment
690 levels; (Riebesell et al., 2011)) in order to maximize the total number of treatment levels at the cost of
691 replication (Zhang et al., 2018). This approach allowed characterizing the response surface as a function of
692 pH. In that study, three populations of coccolithophores were cultured at 11 pH levels for seven
693 generations. Growth rates, POC production rates, and PIC production rates were maximum in a pH range
694 of ~7.75 – 8.15, with differences among populations studied. However, each response metric among all
695 populations declined at the highest pH level of ~8.45 (pCO₂ of ~125 μatm). Generality in outcome among
696 populations and response metrics indicates this is a possible response metric to be considered in mCDR.

697 The last threshold identified from the OA-ICC dataset comes from field experiments in rocky intertidal
698 pools (Dorey et al. 2023). In this study, carbonate chemistry (via DIC manipulation) was manipulated in
699 intertidal pools to investigate effects on net community production and calcification at tidal emersion
700 when tide pools are isolated. During day-time emersion, pH in unmanipulated tide pools can increase to
701 exceed 9 and even 10 pH units. The authors report that in instances where pH exceeded 10 - via near
702 complete consumption of DIC - that saturation states were near zero. In these cases, there was a rapid
703 reversal in net community calcification rates to be negative (dissolution dominant). While this occurred at
704 an extremely high pH in a natural analogue setting, it is a response metric of relevance to mCDR
705 applications and represents a shift in whole community biogeochemical function.

706 3.4.2 Field and applied studies

707 Here, we have grouped studies associated with field observations (mCDR pilot studies and natural
708 analogues) and studies associated with applied issues (OA mitigation, pest control and waste disposal).
709 This is a heterogeneous grouping, but the studies share a tendency to differ in methodology and approach
710 from the species response experiments described in the taxon and OA experiment sections. There are a
711 total of 40 threshold estimates from field/applied studies. There are 8 mortality thresholds, 12 no threshold
712 detected values, 8 population growth thresholds, 7 positive thresholds and 5 sublethal thresholds. There
713 are no LC50 estimates for the field/applied studies. The summary table for field/applied studies with no
714 threshold detected values (Table 6) illustrates some of the data compiled in the database - the complete set
715 of summary tables for field/applied studies are included in the supplemental information (S1: tables 6a-d).

716 **Table 6:** Field and applied studies in which no response was detected when species were exposed to
717 mCDR carbonate chemistry conditions. The “No response detected” column shows the highest pH or
718 alkalinity treatment to which the organism was exposed.



719

Field studies						
No response detected (max exposure)						
Citation	Study type	Taxon	Species	Life stage	Experiment duration	No response detected (max exposure)
Middelboe et al. 2007	Natural variability	Macroalgae	NA (<i>Ulva sp.</i>)	Not_applicable	1 hours	9.3 pH
Hansen et al. 2019	Natural variability	Phytoplankton	Dinoflagellate (<i>Gymnodium dominans</i>)	Not_applicable	72 hours	9.5 pH
Greiner et al. 2018	OA mitigation	Bivalves	Manila clam (<i>Ruditapes philippinarum</i>)	Juveniles	55 days	7.6 pH
Ravaglioli et al. 2024	OA mitigation	Echinoderm	Purple sea urchin (<i>Paracentrotus lividus</i>)	Larvae	72 hours	8.32 pH
Jankowska et al. 2025	Other	Bivalves	Eastern oyster (<i>Crassostrea virginica</i>)	Adult	300 days	~3150 $\mu\text{mol/kg}$
Captura et al. 2025	Other	Bivalves	Mediterranean mussel (<i>Mytilus galloprovincialis</i>)	Adult	96 hours	10.1 pH
Captura et al. 2025	Other	Fish	Pacific topsmelt (<i>Atherinops affinis</i>)	Larvae	7 days	9.8-10.1 pH
Captura et al. 2025	Other	Macroalgae	Giant kelp (<i>Macrocystis pyrifera</i>)	Other	48 hours	9.8-10.1 pH
Brussaard et al. 1996	Other	Phytoplankton	NA (<i>Phaeocystis</i>)	Not_applicable	-	
Brooks et al. 2020	Pest control	Bivalves	Blue mussel (<i>Mytilus edulis</i>)	Adult	10 days	9.16 pH
Brooks et al. 2020	Pest control	Crustacean	Green shore crab (<i>Carcinus maenas</i>)	Adult	10 days	9.16 pH
Brooks et al. 2020	Pest control	Macroalgae	Bladderwrack (<i>Fucus vesiculosus</i>)	Other	10 days	9.16 pH

720

721 mCDR field pilot studies

722 Although a handful of pilot projects have deployed mCDR technologies in the field, we are not aware of
 723 any peer-reviewed published study to date with potential information regarding carbonate chemistry
 724 thresholds. A non-reviewed preprint describing results from an OAE pilot is available (Jankowska et al.,
 725 2025). The Jankowska et al. (2025) study found no effect of olivine addition on biomass changes in
 726 Eastern oysters (*Crassostrea virginica*) placed along a beach on Long Island, NY, USA. Biomass was
 727 reported after 64, 147 and 300 days exposure from oysters at two sites within the olivine placement area
 728 and at control sites at either end of the placement. The highest observed alkalinities at the olivine site
 729 (~3100 $\mu\text{mol kg}^{-1}$) were in sediment porewaters at 14 and 77 days post deployment, though samples were
 730 relatively infrequent making it difficult to determine the duration of the high alkalinity periods. This study
 731 suggests tolerance for this species to alkalinity increases of ~1000 $\mu\text{mol kg}^{-1}$ above ambient conditions for
 732 at least some period of time.



733 Several OAE mCDR pilot projects are underway or have recently been completed that plan to report on
734 biological observations or experiments in the field study area. However, at the time of this review, none
735 had yet published any biological studies. An incomplete list of these projects includes [Loc-ness](#) (WHOI;
736 ship-dispersed NaOH), [Macoma](#) (Ebb Carbon; electrochemical OAE), [Duck](#) (Vesta; olivine sand), and
737 [Tufts Cove](#) (Planetary; alkalinity addition to existing water discharge).

738 Although not completely a field project, a study by Captura, exposed individuals of three species to
739 effluent created at their field-deployed direct ocean capture system. In preliminary findings, a company
740 report (Captura, 2025) describes exposures of up to ~pH 10, that resulted in no mortality to Mediterranean
741 mussels (*Mytilus galloprovincialis*; 96 hr exposure) or Pacific topsmelt (*Atherinops affinis*; 14 d exposure)
742 and no reduction in germination for the spores of giant kelp (*Macrocystis pyrifera*; 48 hr post settlement).

743 There are multiple papers that describe changes in microbes and/or phytoacteria from ocean iron
744 fertilization (OIF) experiments (Arrieta et al., 2004; Assmy et al., 2007; de Baar et al., 2005; Batten and
745 Gower, 2014; Hall and Safi, 2001; Hoffmann et al., 2006; Martin et al., 2013; Quéguiner, 2013; Thiele et
746 al., 2012; Trick et al., 2010; Van Oijen et al., 2005; Yoon et al., 2016). The removal of iron limitation is
747 the primary driver of changes in species composition and abundance in these experiments; any effects of
748 changes in carbonate chemistry are presumed to be non-existent or secondary. If there is an effect of
749 carbonate chemistry, it is impossible to decouple from the effects of iron in these studies given how they
750 were conducted and the data collected. One of the few papers to report relevant carbonate chemistry data
751 (de Baar et al., 2005) describes very small changes in measured pH (+0.033 units), which is not in the
752 range where we would expect a biological threshold.

753 *Natural analogues*

754 Natural analogues can potentially provide insights into biogeochemical processes that may occur if mCDR
755 were to deploy at scale (Bach and Boyd, 2021). For example, a persistent sargassum belt in the Atlantic
756 may serve as an analogue for macroalgae cultivation (Bach et al., 2021) however, there are currently no
757 studies suggesting biological consequences of changes in carbonate chemistry associated with sargassum.
758 As another class of examples, existing seagrass areas may provide insight into biotic mCDR methods
759 focused on macrophytes. Sites in Tanzania with 60-100% eelgrass cover had a mean pH of 8.78 with a
760 calculated pCO₂ of ~30 μatm, but there was no data on biological effects (Job et al., 2023). In California
761 ecosystems, the pH in sites with eelgrass (mean = 7.98, min = 7.46, max = 8.60) are slightly higher than
762 sites without eelgrass (7.91, 7.41, 8.34), but again there was no measure of biological effects (Ricart et al.,
763 2021a) (but see (Van Dam et al., 2021)). In a separate large mesocosm study, the presence of eelgrass



764 raised pH from a mean of 7.93 up to a mean of 8.07 and enhanced the growth of oyster shells (Ricart et
765 al., 2021b).

766 There are several papers that look at natural OIF analogues (Blain et al., 2007, 2008; Robinson et al.,
767 2016). However, the natural OIF analogues do not seem to have any threshold relevant information.
768 Phytoplankton blooms may be natural analogues for OIF or DOCCS since they raise pH by removing DIC
769 (Subhas et al., 2023). The pH in phytoplankton blooms can get relatively high (>9) (Menéndez et al.,
770 2001b; Middelboe and Hansen, 2007). There are some studies that describe secondary biological changes
771 associated with phytoplankton blooms. For example, a study by Brussard *et al.* (1996) observed changes
772 in the microbial community during a bloom in which pH went up to 8.7, though there is no direct causal
773 link. Although studies of analogues may provide information on potential changes in carbonate chemistry
774 from mCDR, we did not find any studies with direct information on carbonate chemistry thresholds.

775 *Ocean acidification mitigation*

776 OA mitigation efforts in the field and in aquaculture hatcheries attempts to locally reverse the deleterious
777 effects of low pH/high pCO₂ from OA either by adding alkalinity or by removing CO₂. In these studies,
778 CO₂ is generally reduced by increasing photosynthesis through increased production of macroalgae or
779 marine plants (Clements and Chopin, 2017; Fernández et al., 2019).

780 Contrary to expectations, a study growing eelgrass or *Ulva* and clams together in Puget Sound found
781 lower pH and smaller clams in the presence of eelgrass (Greiner et al., 2018). Another study in Puget
782 Sound found oysters grew better in kelp, but did not see any change in mean pH; the oyster performance
783 was attributed to increased pH stability and more food in kelp (Bednaršek et al. 2024). An experiment
784 rearing clams, mussels and oysters in Long Island, NY found increased growth in areas with kelp where
785 pH increased from pH ~7.2 without kelp to a max of ~8.8 in kelp (Young et al., 2022).

786 In some locations, shellfish hatcheries buffer seawater to raise pH in an effort to increase larval survival
787 (Barton et al., 2015; Clements and Chopin, 2017; Lewis-Smith et al., 2025; Mackenzie et al., 2022). In
788 one study, counter to the expectation of OA mitigation, larvae with pH buffered to ~8.1 had an altered
789 microbiome and lower survival when challenged with heat wave or *Vibrio* compared to larvae grown in
790 ambient pH ~7.8 conditions (Mackenzie et al., 2022). The Puget Sound Restoration Fund hatchery at the
791 NOAA Northwest Fisheries Science Center Manchester Station sets a target of pH 7.8-8 when buffering
792 (i.e., won't buffer unless <7.8) and the PacHybreed hatchery at the Manchester Station tries to keep the pH
793 around 7.8 to 8.5, but ideally closer to 8-8.1 (pers. com. M Gavery).



794 A field study evaluated the extent to which alkalinity enhancement reduced the effects of OA on a coral
795 reef (Albright et al., 2016). In this study, NaOH (~50 $\mu\text{mol kg}^{-1}$ max) was repeatedly applied to the reef for
796 elevated alkalinity exposures to several hours. This exposure resulted in increasing the pH from ~8.05 to
797 8.35 with an associated 17% increase in calcification.

798 *Pest/parasite control*

799 Quicklime (calcium oxide) has been used as a pest control method to kill sea urchins overgrazing kelp
800 (Strand et al., 2020), seastars preying on harvested bivalves (Shumway et al., 1988b), tunicates fouling
801 aquaculture structures (Locke et al., 2009), and salmon louse parasitizing salmon aquaculture (Ciani et al.,
802 2025). A number of studies have been conducted to evaluate the efficacy of quicklime to kill the target
803 organism and toxicity to non-target components of the marine ecosystem (See tables S1-6a and S1-6d).
804 For pest control, quicklime is spread as fine or coarse particles in the area to be treated (Brooks et al.,
805 2020). Although quicklime is a strong base and will raise the pH in the area of deployment, the primary
806 mechanism by which quicklime kills the target species (and any other vulnerable species in the vicinity) is
807 believed to be by the corrosive action of direct contact with quicklime particles, not necessarily changes in
808 seawater pH. Because it is a strong base, dissolves readily in seawater and could potentially be produced
809 on a large scale by the cement industry, quicklime has been proposed as a source of alkalinity for OAE
810 (NASEM, 2022). Although some proposed OAE methods would first dissolve the quicklime to be
811 dispersed as a concentrated liquid, other methods consider dispersing it as a solid (Caserini et al., 2021),
812 which could subject organisms to contact with solid quicklime. Our threshold evaluation for pest control
813 studies (Tables S1-6a and S1-6d) is based on pH measured in seawater during quicklime dosing
814 experiments. It is not possible in these experiments to separate the effects of changes in seawater pH from
815 caustic effects of contact with quicklime particles, so these estimates have an elevated level of uncertainty.
816 Also, given the methods of these studies, the carbonate chemistry was almost certainly not in equilibrium,
817 so pH likely changed constantly during the exposure, with pH values reported in the studies representing
818 only a snapshot of highly dynamic pH conditions. We did not attempt to estimate thresholds for direct
819 contact with quicklime. Sensitivity seems very species specific and heavily influenced by level of contact.

820 *Waste disposal*

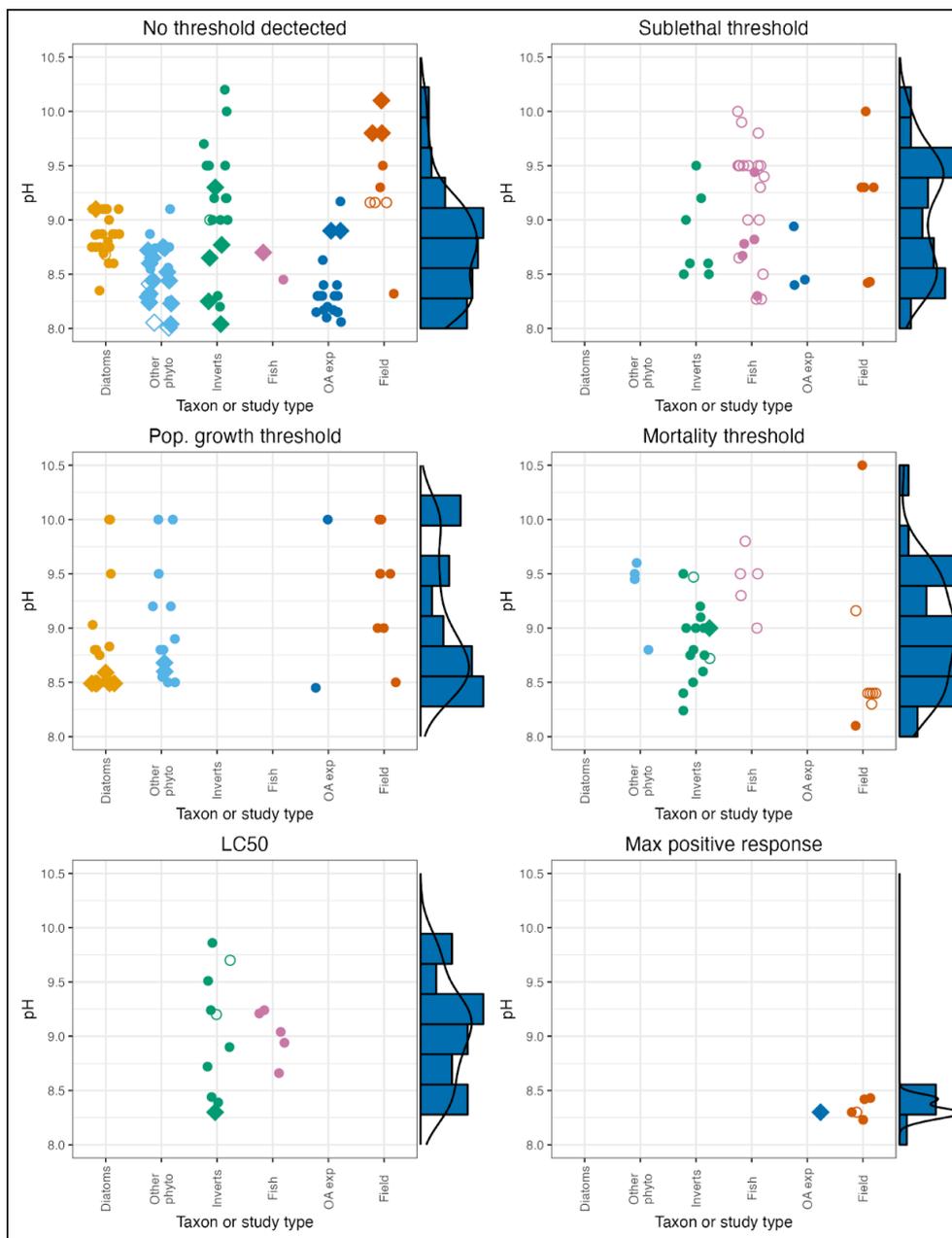
821 The disposal of alkaline industrial waste at sea can potentially provide information about biological
822 response to elevated pH. For example, alkaline aluminate wastes dumped in the North Sea (Vandelannoote
823 et al., 1987) formed a precipitate and raised the pH, in some places measured at 8.9. However, no
824 biological studies accompanied this observation. In the only alkaline industrial waste study we identified
825 with potential threshold information, microbial samples were analyzed from near corroding barrels that



826 contained material associated with the manufacture of DDT (Gutleben et al., 2025). The barrels, located in
827 a deep-sea basin near Los Angeles, were >40 years old and the contents raised the pH of surrounding
828 sediments and waters above pH 12. Some alkaliphilic microbes persisted in these high pH conditions,
829 though species composition shifts occurred at lower pH levels.

830 3.5 Threshold synthesis

831 The threshold estimates were most commonly presented in terms of pH ($n = 231$) rather than in alkalinity
832 or other units, and the collected pH threshold levels are compiled in Figure 7. For reasons described in the
833 discussion, we did not attempt any statistical analysis of the data presented in Figure 7. The maximum pH
834 exposure with no detectable response ranges from slightly above ambient for experiments that did not
835 involve very high pH to pH 12.7 for an invertebrate species that appears extremely tolerant of high pH
836 under some experimental conditions. The highest maximum exposures occurred for invertebrate species
837 and in field observations, though we emphasize again that these data do not represent maximum tolerance,
838 but are the maximum conditions under which species were exposed. It is interesting to note that just a
839 single study on fish reported no threshold detected values. Sublethal thresholds were estimated for
840 invertebrates, fish and the OA experiments with overall ranges between 8.25 and 10. Population growth
841 rate thresholds were estimated primarily for phytoplankton studies, where population is a common
842 response metric, though some OA experiments and field observations also evaluated population growth.
843 The overall range for population growth thresholds is pH ~8.5-10. Mortality thresholds from invertebrates
844 span a similar range as for invertebrate sublethal thresholds pH ~8.25-9.5. The mortality threshold range
845 for fish is higher than for invertebrates (pH ~9-9.8). The mortality threshold estimates for field studies is
846 substantially lower (pH ~ 8.25-8.4), but the primary stressor in those studies may not have been pH (see
847 field section). A wide range of LC50 values were estimated for invertebrates (pH ~8.3-9.8), with only two
848 LC50 for fish (pH ~ 8.7 and 8.9). A positive effect of pH above ambient levels was observed in six cases,
849 just 3% of the total. Only three studies report a positive response with reported values of pH ~8.25.



850

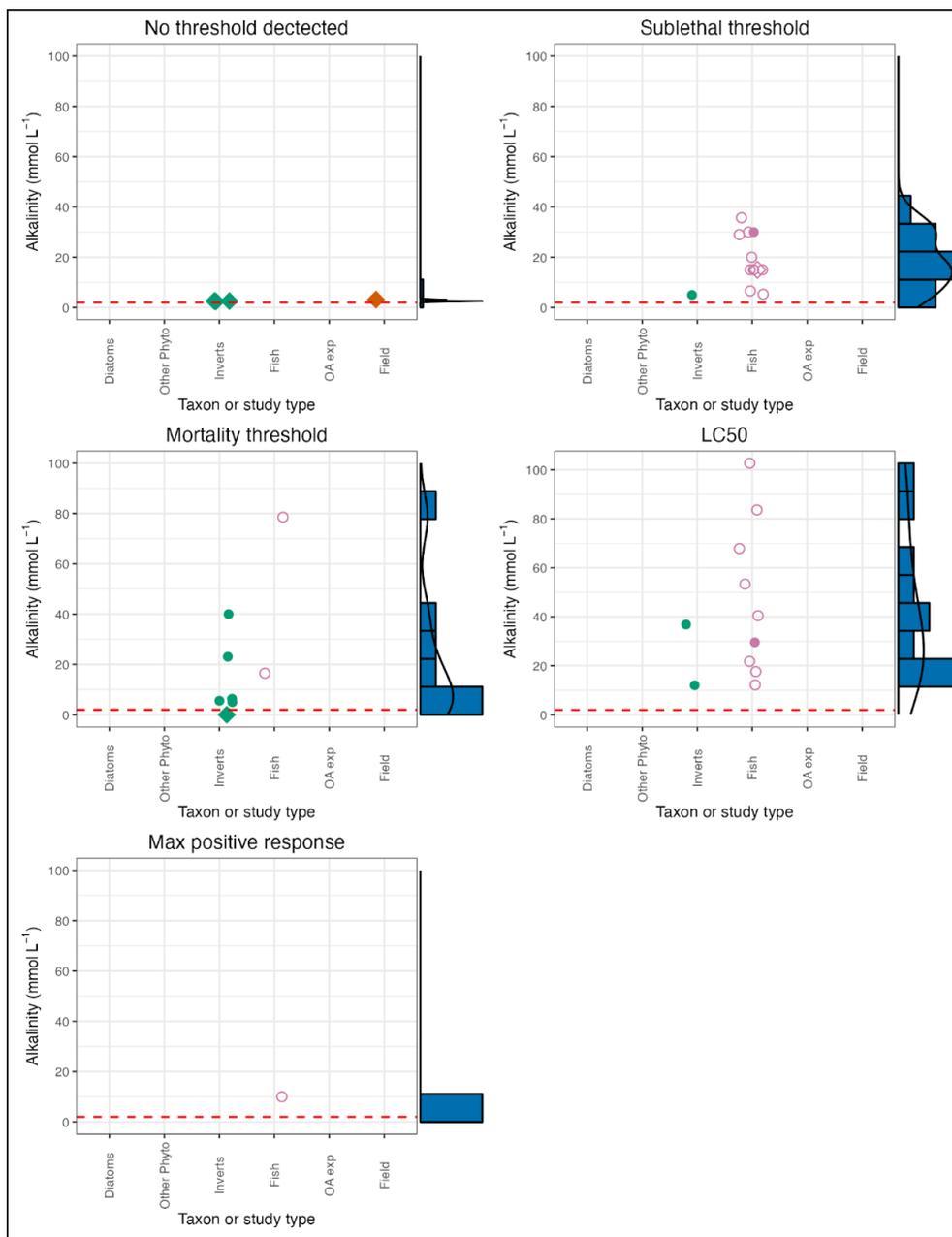
851 **Figure 7:** Threshold pH values for various taxa and study types from studies in the mCDR carbonate



852 chemistry database. In the x-axis labels, "Other phyto" refers to other phytoplankton (not diatoms),
853 "Inverts" to invertebrates, "OA exp" to OA experiments, and "Field" to field studies. The "No threshold
854 detected" values are the pH values tested in experiments or observations in which no species response
855 occurred. The sublethal, population growth and mortality threshold are the first level or observation in a
856 study in which species response was statistically different from ambient control or reference. There were
857 two high pH values in the database not included in the figure to provide more visual resolution in the pH
858 8.0-10.5 range. The excluded values were for Invert no-threshold-detected (pH 12.7) and fish mortality
859 threshold (pH 12.23). The colors in the plot are for visual separation and tracking of the taxa or study type.
860 The figure only includes the subset of studies in the data base that expressed results in terms of pH. The
861 large diamond points are from studies that explicitly considered a specific mCDR method, whereas the
862 circles show data from non-mCDR studies. The open shapes indicate estimates with qualitatively assessed
863 very high uncertainty because there were experimental confounding factors (e.g. contact with particulate
864 quicklime), the experiment was on a freshwater species (mostly fish) or other factor.

865

866 Although less common than pH, some studies ($n = 37$) contain data for threshold estimates for alkalinity
867 (Figure 8). The estimates are primarily from studies on fish ($n = 23$), with some on invertebrates ($n = 13$)
868 and a single estimate from field/applied studies. The threshold estimates for fish in particular show an
869 extremely wide range of alkalinity. One fish study estimated an LC50 ~50 times the current surface
870 alkalinity levels, suggesting a very high tolerance for high alkalinity for some species. For a few studies (n
871 = 9), data were available to estimate both pH and alkalinity thresholds. There are very few joint
872 pH/alkalinity data on which to draw conclusions, but there is no statistical relationship between pH and
873 alkalinity of exposures, which perhaps reflects the variety of ways in which experimental conditions are
874 generated and measured and different states of carbonate chemistry system equilibrium (Supplemental
875 Figure S1-1).



876



877 **Figure 8:** Threshold alkalinity values (mmol L^{-1}) for various taxa and study types from studies in the
878 mCDR carbonate chemistry database. In the x-axis labels, "Other phyto" refers to other phytoplankton
879 (not diatoms), "Inverts" to invertebrates, "OA exp" to OA experiments, and "Field" to field studies. Each
880 point represents the threshold estimate for a single study. The colors indicate taxon or study type to
881 provide visual continuity across plot panels. The "No threshold detected" values are the alkalinity values
882 tested in experiments or observations in which no species response occurred. The sublethal, population
883 growth and mortality threshold are the first level or observation in a study in which species response was
884 statistically different from ambient control or reference. For reference, the horizontal dashed line shows
885 the approximate current ocean surface alkalinity (2 mmol L^{-1}). The large diamond points are from studies
886 that explicitly considered a specific mCDR method, whereas the circles show data from non-mCDR
887 studies. The open shapes indicate estimates with qualitatively assessed very high uncertainty because
888 there were experimental confounding factors (e.g. contact with particulate quicklime), the experiment was
889 on a freshwater species (mostly fish) or other factor.

890

891 **4 Discussion**

892 **4.1 Thresholds for mCDR**

893 Reviewing the literature on biological responses to mCDR carbonate chemistry conditions reveals the
894 challenges in estimating biological thresholds. The collected studies demonstrate a high variability in
895 sensitivity among species and also the profound limitations of available data. For example, multiple taxa
896 do not show any sensitivity at pH values greater than 9, while some show no sensitivity at pH greater than
897 12 (Figure 7). These "no detect" studies illustrate one of the issues with interpreting available data: these
898 values do not represent the maximum tolerable values, they are only the highest treatment levels used in
899 the experiments. In some experiments, the maximum pH tested was only 8.3 (or less). Although these
900 treatments are greater than mean ambient pH and therefore provide some information about sensitivity to
901 mCDR, they are within the range of natural variability and do not provide much data for defining a
902 threshold.

903 Likewise, studies that do detect a biological response in mCDR-like conditions, generally do not describe
904 a true threshold, but rather indicate the experimental level at which a response was first observed. Given
905 that most of the studies consisted of just a few levels (sometimes only 2) or a very small range even with
906 multiple levels, it is not possible to determine the species response curve (Figure 1) and therefore not
907 possible to determine the actual threshold level. In some studies, only LC50 or LC10 was reported, which,



908 although a common metric in toxicological studies, does not define a threshold as we are using the term
909 here and does not provide any information on the species response curve.

910 It is difficult to summarize the study threshold values presented in Figures 7 and 8. As noted above, the
911 studies may have limited information about chemical concentrations at which a species actually begins to
912 respond to mCDR conditions. The studies also vary substantially in treatment method (e.g., how the
913 manipulation was performed; feedstocks applied; experimental set up), duration of exposure, carbonate
914 system equilibration status, response metrics, and approaches to statistical analysis. This variation in study
915 methodology arises because the majority of studies were not designed to address mCDR. Any attempts to
916 average the values or apply some other summary statistic to the data in Figure 7 would be statistically
917 inappropriate. The studies have different sample sizes, numbers of replicates and experimental design
918 (replicates vs gradient approach), and may lack independence because in some cases, the data are from
919 different species exposed as part of the same experiment. As discussed below, a formal meta-analysis
920 could address these statistical issues, but at a cost of greatly limiting the number of studies considered.

921 Although we are not drawing statistical conclusions from figure 7, it is possible to make some general
922 observations. 1) There is a large range in the pH levels that different species can tolerate without any
923 detectable response to elevated pH. Some species seem able to tolerate the pH conditions that may be
924 commonly generated by mCDR, at least for limited amounts of time for the responses measured in
925 existing studies. 2) For species with threshold estimates, there is a wide range in pH values (~ 8.3-12.5)
926 with no distinct “safe/unsafe” level. 3) The few studies that show a positive response seem to do so at
927 ~8.3 pH. However, this is also a range in which some species have a mortality threshold, so it should not
928 be assumed that this level is beneficial (or neutral) for all species.

929 Our approach to mCDR thresholds differs from that of Bednaršek et al. (2025), which focused on
930 calcifiers in the context of OAE. Bednaršek et al. (2025) extrapolated species calcification response from
931 existing OA studies into the TA:DIC ratio space expected from OAE, in some cases extrapolating from
932 OA treatments with ratios below ambient conditions. Based on their analysis, they suggest a regulatory
933 threshold of pH 9. Our data presentation does not rely on any extrapolation and we do not suggest a
934 regulatory threshold. The analysis by Bednaršek et al. (2025) was used as a starting point to evaluate the
935 potential of OAE to mitigate OA (van de Mortel et al., 2026), which reveals an inherent trade-off: as OAE
936 becomes more effective at removing atmospheric CO₂, its capacity to mitigate the biological impacts of
937 OA on calcifiers diminishes.



938 We find that the available data do not support the identification of a single high pH or high alkalinity
939 threshold that can be applied to all taxa or to specific taxon groups. In our analysis, there is no obvious
940 biological tipping-point for species sensitivity. We have therefore restricted our threshold analysis to
941 presenting distributions of threshold estimates from individual studies and have not picked a single
942 threshold number or set of numbers from those distributions as somehow “the” threshold. We recognize
943 that this may be unsatisfying from the perspective of mCDR management and regulation, which often rely
944 on discrete values for setting permit limits or monitoring requirements. However, our analysis does
945 provide a useful starting point for developing experimental protocols for threshold identification as well as
946 management recommendations, which could use this synthesis of available information in combination
947 with a policy-informed application of precautionary principles to establish interim guidelines.

948 **4.2 Recommendations for future research**

949 Reviewing existing studies revealed substantial gaps in current understanding and motivated suggestions
950 for how to develop better estimates of biological thresholds for mCDR-induced changes in carbonate
951 chemistry. A first recommendation is further analysis of existing studies, using our database, and the
952 references therein, as a starting point. For our analysis, we extracted information in the format it was
953 presented in the studies and did not attempt a statistical meta-analysis. A formal meta-analysis would
954 involve estimating effect sizes for each of the study responses and would provide a statistical framework
955 for combining experiments with different sample sizes, underlying variance and confounding random
956 effects (e.g., studies of different species co-occurring in the same experiment) (Borenstein et al., 2021;
957 Viechtbauer, 2010). A meta-analysis of these studies would likely be productive; however studies would
958 need to undergo a careful selection process to ensure that they contained the proper data for meta-analysis
959 and that they are comparable in terms of experimental methods, treatment variables, and response metrics.
960 A meta-analysis would provide statistical rigor but at a cost of considering only a small subset of the
961 available information. In cases targeting a specific focal group, like marine fish larvae, there are likely not
962 enough comparable data to conduct a meta-analysis at all. The summary of available information, as
963 provided in this study, allows for different insights than a meta-analysis on a subset of studies. The
964 database we have compiled can also be used as a first step in identifying studies that could be appropriate
965 for inclusion in a meta-analysis.

966 One of the challenges we faced in identifying thresholds was the limited number of pH (or alkalinity)
967 treatment levels typically included in experimental studies. Experimental scientists have traditionally
968 implemented Analysis of Variance (ANOVA) experimental designs, which test differences in response
969 means among discrete treatment groups. A strength of this type of experimental design is its emphasis on



970 replication, which provides strong statistical power, clear hypothesis testing, and well-established
971 inferential frameworks. This rigor makes this design and statistical tools used with resulting data
972 particularly effective for detecting differences among treatments. However, the need for high replication
973 typically constrains the number of treatment levels (see for example (Kousoulas et al., 2025)) that can be
974 tested, which can limit ecological or mechanistic realism when responses vary continuously across
975 environmental gradients. As a result, this type of experiment often provides only coarse insight into
976 response behavior and has limited ability to characterize thresholds across a response surface (Cottingham
977 et al., 2005). In contrast, response-curve experimental designs trade replication for broader coverage of the
978 experimental space, enabling more direct estimation of functional relationships and response surfaces
979 across continuous gradients. While this can reduce power at individual treatment levels and complicate
980 statistical inference, it can reveal thresholds. An exemplary study implementing a response-curve study
981 design is that of Zhang et al. (2012), testing 11 treatment levels of pH between 7.3 and 8.45.

982 One specific gap identified in our analysis was the limited data on thresholds related to egg fertilization in
983 broadcast spawners. Seawater pH plays a critical role in reproduction and fertilization of
984 broadcast-spawning marine invertebrates and fish because these early life processes occur externally and
985 are directly exposed to ambient carbonate chemistry. A few studies on various species of limpets
986 highlighted higher fertilization rates with increasing pH, with a potential threshold between pH 9 and 10
987 depending on the species (Aquino De Souza et al., 2009; Cañizares et al., 2021; Castejón et al., 2021;
988 Guallart et al., 2020). However, we did not identify any studies that test the effects of elevated pH levels
989 (above current conditions whether by alkalinity addition or DIC reduction) on reproduction and
990 fertilization for other broadcast-spawning taxa. Reduced pH associated with ocean acidification can impair
991 multiple stages of reproduction, beginning with gametogenesis and extending through fertilization success
992 and early embryonic development (Ross et al., 2011). In many taxa, pH alters sperm motility, swimming
993 speed, and longevity, often reducing the probability that sperm encounter and successfully fertilize eggs at
994 low pH. Further, low pH can affect eggs and zygotes through changes in membrane integrity, intracellular
995 pH regulation, and ion balance, which can lead to abnormal cleavage or delayed development (Ross et al.,
996 2011). However, some tunicate species also maintain acidic conditions (pH 5.5-6.8) in their gonoducts for
997 gamete activation to only occur upon spawning in ambient pH seawater (Sensui et al., 2023). The effects
998 of elevating pH on any of these processes is a current knowledge gap for mCDR applications.

999 Another gap quantified in our analysis was the general lack of long-term studies. Most studies were of
1000 relatively short duration, which may represent an exposure during a pulse mCDR process or a mobile
1001 organism transiting through the plume of a mCDR process outfall. However, sedentary organisms near an



1002 outfall or planktonic/mobile organisms encountering a geographically widespread mCDR process may be
1003 subject to the type of chronic exposure not captured in existing studies. Short duration studies make it
1004 difficult to distinguish between acclimation responses and negative sub-lethal effects. For example, a
1005 change in internal acid-base balance caused by changes in seawater carbonate chemistry may be a sign of
1006 a harmful effect or it could be a normal acclimation process and an indicator of stress. Longer-term,
1007 multi-generational studies could also explore the potential for adaptive evolutionary responses. As
1008 demonstrated by OA experiments, studies on adaptation to carbonate chemistry conditions can be very
1009 challenging, but can also provide insight into long-term biological response (Johnson, 2022; McElhany et
1010 al., 2025; Schlüter et al., 2014; Sunday et al., 2014).

1011 In initiating this project, we considered biological responses to any of the carbonate system parameters
1012 that may be altered by mCDR (Box 2 table and Table 1). However, the analysis primarily focused on pH
1013 since it was by far the most common measure available across studies. Although measures other than pH
1014 may be more relevant to biological or oceanographic processes (Bednaršek et al. 2025), pH is likely to
1015 remain the most practical parameter for assimilating information from existing studies with new
1016 information from species exposure experiments and monitoring of mCDR pilot projects. While our
1017 analysis focused on identifying thresholds in terms of absolute pH or alkalinity values, an equally valid
1018 approach that appropriately acknowledges the regional, local, seasonal and diurnal patterns of carbonate
1019 chemistry variability (Carstensen and Duarte, 2019; Jiang et al., 2019; Torres et al., 2021) could use a pH
1020 offset (ΔpH) threshold expressed as pH units above baseline. One reason we did not pursue estimating
1021 ΔpH thresholds was the difficulty in identifying the baseline reference pH in many of the studies. As a
1022 practical matter, the application of ΔpH thresholds in a management context in the field would likely
1023 experience the same challenge in identifying the baseline reference condition, but could lead to more
1024 biologically grounded thresholds. We also note that pH is a log scale, which may obscure relative
1025 differences in species response to hydrogen ion concentration - future analysis may consider presenting
1026 results directly in the $[\text{H}^+]$ scale.

1027 Future research could benefit from a focus on three areas that would clarify the relationship between
1028 species and mCDR conditions: 1) understanding which carbonate chemistry parameters are actually
1029 driving biological responses, 2) testing organisms in the carbonate chemistry conditions and for exposures
1030 actually generated by specific mCDR process, and, conversely, 3) exploring standardized testing
1031 procedures. Understanding the carbonate system parameters driving biological response (as in Ferderer et
1032 al. (2025)) will aid in understanding physiological processes and aid in extrapolation to untested species
1033 and novel chemistries. Understanding carbonate system drivers can also aid in the development of new



1034 types of management and monitoring thresholds. Although pH is currently the most practical metric, many
1035 mCDR projects will require substantial new carbonate chemistry monitoring to meet MRV requirements
1036 (Halloran et al., 2025). Future threshold development can perhaps anticipate what field data on the
1037 biologically relevant parameters will be available for the creation of management guidelines.

1038 The need to test organisms in the carbonate chemistry conditions of specific mCDR methods and for
1039 plausible duration scenarios is both an opportunity and a challenge. The opportunity is that using the
1040 actual chemistry, including the crucial changes in chemistry during equilibration, and the actual species
1041 exposure patterns will ground the evaluation in real-world tests of species sensitivity. The challenge is that
1042 each mCDR process, even if of the same general type, like OAE, is unique, leading to potentially a very
1043 large number of tests and difficulties in extrapolating to new mCDR scenarios. The path forward is to test
1044 specific mCDR scenarios and, in parallel, to explore potential standardization of testing methodology. The
1045 field of toxicology has a long history of developing standard testing protocols to inform management
1046 decisions (e.g., LC50 tests; e.g., (USEPA, 2015)). There have already been some efforts standardizing
1047 studies on the sensitivity of marine species to mCDR conditions (Iglesias-Rodríguez et al., 2023; Oschlies
1048 et al., 2023) and there are lessons to be learned from the study of OA. Some early efforts at standardizing
1049 OA biological research may have been overly prescriptive and ignored natural variation in environmental
1050 conditions and species behaviors (Barry et al., 2010), but ongoing efforts at standardization helped create
1051 more comparable and statistically valid studies (Cornwall and Hurd, 2015; McElhany and Shallin Busch,
1052 2013). The path forward seems to be an all-of-the-above strategy with both mCDR process specific
1053 studies and the development of standardized protocols, in addition to experiments focused on
1054 understanding the physiological mechanism driving response to mCDR-like changes in carbonate
1055 chemistry.



1056

1057 List of Supplemental Materials

- 1058 • Supplemental tables and figures (S1)
- 1059 • mCDR threshold database csv file
- 1060 • mCDR threshold categories xlxs file
- 1061 • Bibliography of citations in mCDR threshold database pdf file
- 1062 • Bibliography of citations in mCDR threshold database ris file

1063 Author contributions

1064 **Paul McElhany:** Conceptualization, Methodology, Software, Validation, Formal analysis, Investigation, 1065 Resources, Data curation, Writing - original draft, Writing - review & editing, Visualization, Supervision, 1066 Project administration, Funding acquisition. **Mattias Cape:** Investigation, Writing - original draft, Writing 1067 - review & editing, Supervision. **Giulia Faucher:** Conceptualization, Validation, Investigation, Data 1068 curation, Writing - original draft, Writing - review & editing. **Christina Frieder:** Investigation, Data 1069 curation, Writing - original draft, Writing - review & editing, Supervision. **Lenaïg Hemery:** Investigation, 1070 Data curation, Writing - original draft, Writing - review & editing. **Debora Iglesias-Rodriguez:** 1071 Conceptualization, Investigation, Writing - original draft, Writing - review & editing. **Christopher 1072 Murray:** Investigation, Data curation, Writing - original draft, Writing - review & editing. **Wesley Noble:** 1073 Software, Investigation, Data curation, Writing - review & editing.

1074 Competing interests

1075 The authors declare that they have no conflict of interest.

1076 Disclaimer

1077 The scientific results and conclusions, as well as any views or opinions expressed herein, are those of the 1078 author(s) and do not necessarily reflect the views of NOAA or the Department of Commerce.

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