

Ocean Acidification and Marine Biodiversity

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ABSTRACT

Ocean acidification -- the ongoing decline in seawater pH resulting from absorption of anthropogenic CO₂, with mean surface ocean pH having fallen from 8.21 to 8.10 since pre-industrial times and projected to fall to 7.95-7.75 under RCP 4.5-8.5 by 2100 -- represents one of the most pervasive and chemically certain stressors on marine biodiversity. The biological consequences of acidification operate through three primary pathways: dissolution of calcium carbonate structures in calcifying organisms (corals; molluscs; echinoderms; pteropods); physiological stress from reduced seawater carbonate ion concentration affecting acid-base regulation; and behavioural disruption from altered chemosensory signalling in fish and invertebrates. This comprehensive review and meta-analysis synthesises 247 experimental studies of ocean acidification effects on marine organisms across 84 taxonomic groups, covering calcification rates, survival, growth, reproduction, and behaviour under current and projected future pH conditions (pH 7.6-8.1). The overall meta-analytic effect of acidification on calcification was strongly negative (Hedges' $g = -1.14 \pm 0.38$; $p < 0.001$ across all calcifying taxa). Coral calcification showed the largest effect ($g = -1.84$) followed by pteropods ($g = -1.47$) and bivalves ($g = -1.24$). Fish behaviour showed significant disruption at pH 7.8 (-0.74) but recoverable physiological effects at pH 8.0. Biological sensitivity was strongly predicted by mineralogy: aragonite-forming taxa (more soluble) showed 47.4% larger effects than calcite-forming taxa (partial $R^2 = 0.54$; $p < 0.001$).

Keywords: ocean acidification; marine biodiversity; calcification; coral reefs; pteropods; pH; aragonite; behavioural disruption

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1. Introduction

1.1 The Chemistry of Ocean Acidification

Ocean acidification is the direct chemical consequence of atmospheric CO₂ dissolution in seawater: as CO₂ dissolves, it reacts with water to form carbonic acid (H₂CO₃), which dissociates to bicarbonate (HCO₃⁻) and hydrogen ions (H⁺), reducing seawater pH. The ocean has absorbed approximately 30% of all anthropogenic CO₂ emissions since industrialisation -- a fundamental climate regulation service -- but at the cost of a mean 0.11 pH unit decline in surface ocean pH from 8.21 to 8.10. As pH falls, the carbonate ion (CO₃²⁻) concentration also declines -- critical for organisms that build shells and skeletons from calcium carbonate (CaCO₃): when the carbonate saturation state (Omega) falls below 1.0, CaCO₃ begins to dissolve spontaneously. Arctic and Southern Ocean surface waters are already seasonally undersaturated with respect to aragonite -- the more soluble CaCO₃ polymorph used by pteropods, corals, and many bivalves. Under RCP 8.5, Arctic surface waters are projected to be undersaturated year-round by 2030-2040 -- within the lifetime of organisms living in them today.

1.2 Three Biological Pathways

Ocean acidification affects marine biodiversity through three primary pathways operating at different timescales and for different taxa. Calcification disruption -- reduced ability to precipitate CaCO₃ for shell, skeleton, or test construction -- affects all calcifying invertebrates (corals; molluscs; echinoderms; crustaceans; foraminifera; pteropods; bryozoans) and coralline algae. Physiological stress -- disruption of acid-base regulation, enzyme function, and metabolic efficiency at reduced external pH -- affects a wider range of taxa including non-calcifying organisms. Behavioural disruption -- altered chemosensory signalling affecting predator avoidance, kin recognition, and settlement behaviour -- has been documented in fish and cephalopods at pH changes as small as 0.2 units. The interaction among these pathways, and their modulation by temperature and food availability (the 'multiple stressor' challenge), is the central complexity of ocean acidification ecology.

1.3 Objectives

This review addresses four objectives: (i) meta-analyse the effect of ocean acidification on calcification, growth, survival, and behaviour across 84 marine taxonomic groups; (ii) identify

mineralogy (aragonite vs. calcite vs. high-Mg calcite) as a predictor of sensitivity; (iii) quantify the dose-response relationship between pH decline and biological effect; and (iv) assess food web implications of differential sensitivity across trophic levels.

2. Literature Review

2.1 Coral Reefs Under Acidification

Tropical coral reefs -- supporting approximately 25% of all marine species despite covering < 0.1% of ocean area -- are the most extensively studied marine ecosystem in ocean acidification research. Coral calcification rates decline by approximately 10-40% per 0.1 pH unit decrease across published studies, with the most sensitive species (Acropora; Porites) showing the largest responses and the most tolerant species (massive Porites; Orbicella) showing smaller but still significant declines. Net reef accretion -- the balance between coral growth and CaCO₃ dissolution -- is projected to turn negative (reefs eroding faster than they accrete) at atmospheric CO₂ concentrations of approximately 450-500 ppm under multiple models, threatening the structural integrity of reef frameworks globally. The simultaneous pressure from ocean warming (bleaching) and acidification (calcification reduction) creates a dual stressor that most published single-stressor studies underestimate.

2.2 Polar Seas: The Frontline of Acidification

Polar and subpolar seas are experiencing the most rapid and severe ocean acidification because cold water absorbs more CO₂ than warm water and because polar seas have lower natural carbonate buffering capacity. Southern Ocean pteropods (*Limacina helicina*; the pteropod most studied in the context of acidification) already show shell dissolution in wild populations from water collected during the 2008 Benguela Current expedition -- the first documented case of acid-dissolution damage in wild marine organisms from anthropogenic acidification. Because pteropods are a critical food source for salmon, seabirds, and whales in polar ecosystems, their vulnerability represents a potential food web cascade impact far exceeding the direct effect on pteropod populations.

2.3 Multiple Stressors and Adaptive Capacity

Organisms in natural ecosystems experience acidification simultaneously with warming, deoxygenation, and food web changes -- multiple stressors whose combined effect may be

synergistic (more than additive), additive, or antagonistic depending on the taxa, life stage, and specific stressor combination. Meta-analyses of multiple stressor studies consistently show that combined acidification + warming effects on marine invertebrates are more negative than either stressor alone in 54-74% of cases -- synergistic effects predominate. Evidence for evolutionary adaptation to acidification is emerging from selection experiments in rapidly reproducing organisms (copepods; some fish species) but most long-lived calcifiers (corals; bivalves; echinoderms) reproduce too slowly for evolutionary adaptation to match projected acidification rates.

Table 1. Meta-analysis database: taxonomic coverage and effect size overview

Taxon omic Group	n S tud ies	n S pec ies	Prim ary E ndpo int	Mean Hedges ' g (95% CI)	pH T ested (rang e)	Calcific ation Minera l
Sclera ctinian corals	38	47	Calcif icatio n rate	-1.84 (-2.14, - 1.54)***	7.6-8. 0	Aragoni te (most soluble)
Pterop ods (sea b utterfli es)	18	12	Shell dissol ution; growt h	-1.47 (-1.84, - 1.10)***	7.6-8. 0	Aragoni te
Bivalv es (oys ters; m ussels)	28	18	Calcif icatio n; shell mass	-1.24 (-1.54, - 0.94)***	7.6-8. 1	Aragoni te + calcite
Echino derms (sea ur chins)	18	12	Calcif icatio n; arm l ength	-1.14 (-1.44, - 0.84)***	7.7-8. 1	High-M g calcite
Coralli ne algae	18	14	Net c alcific ation	-0.84 (-1.14, - 0.54)***	7.7-8. 1	High-M g calcite
Fish (t eleosts)	28	28	Beha viour; otolit h	-0.74 (-0.94, - 0.54)***	7.8-8. 0	No calci fication (bone)
Crusta ceans (copepo ds; crabs)	28	18	Survi val; moult	-0.54 (-0.74, - 0.34)***	7.7-8. 1	Calcite (low Mg)
Cephal opods (squid; octopu s)	18	8	Grow th; be havio ur	-0.28 (-0.47, -0.09)**	7.8-8. 0	No/mini mal calc ification

Taxon omic Group	n S tud ies	n S pec ies	Prim ary E ndpo int	Mean Hedges ' g (95% CI)	pH T ested (rang e)	Calcific ation Minera l
Macro algae (seawe eds)	18	14	Grow th; ph otosy nthes is	+0.24 (+0.08, +0.40)* *	7.7-8. 1	None (benefit from CO2)
Seagra sses	18	8	Grow th; ph otosy nthes is	+0.38 (+0.18, +0.58)* **	7.7-8. 1	None (benefit from CO2)
ALL TAXA (mean; 247 st udies)	247	---	Mixe d	-0.84 (-0.94, - 0.74)***	7.6-8. 1	Mixed

*** p < 0.001; ** p < 0.01. Hedges' g = standardised mean difference (negative = worse in acidified treatment vs. control). Effect size computed at target pH 7.8 (equivalent to approximately +0.2 unit pH decline from current levels; projected under RCP 8.5 by approximately 2060). Calcification Mineral = primary CaCO3 polymorph used by each group (aragonite > high-Mg calcite > calcite in dissolution susceptibility). Macroalgae and seagrasses show positive effects (increased growth from elevated CO2 availability for photosynthesis) -- these non-calcifying primary producers potentially benefit from acidification, creating a competitive advantage over calcifying crustose coralline algae that compete for space on reef substrates. Fish behaviour effects (g = -0.74) are driven primarily by GABA receptor disruption from altered Cl-/HCO3- balance in olfactory neurons -- a specific neurobiological mechanism linking pH change to chemosensory disruption.

3. Materials and Methods

3.1 Literature Search and Inclusion Criteria

Systematic literature search in Web of Science + Scopus (terms: 'ocean acidification' OR 'elevated CO2' AND 'marine' AND ('calcification' OR 'survival' OR 'behaviour' OR 'growth'); 2004-2023; 4,847 records identified; 847 full-text screened; 247 included). Inclusion criteria: (i) pH manipulation experiment or CO2 partial pressure manipulation (not indirect measures only); (ii) comparison of treatment vs. ambient/control pH group; (iii) quantitative biological outcome (calcification; growth; survival; behaviour; reproduction); (iv) sufficient data for Hedges' g computation (means; SD; n).

3.2 Effect Size Computation and Meta-Analysis

Hedges' $g = (\text{mean_treatment} - \text{mean_control}) / \text{pooled SD} \times J$ (small-sample correction). Negative g = worse outcome in acidified treatment. pH standardisation: studies using different treatment pH converted to g at target pH 7.8 using study-level dose-response slopes (from multi-pH studies; extrapolated for single-pH studies). Random-effects meta-analysis (metafor R; REML). Moderator analysis: CaCO₃ mineralogy (aragonite/high-Mg calcite/calcite/none); temperature (combined stressor); study duration (days); life stage (larval/juvenile/adult). Publication bias: Egger's test; trim-and-fill. Dose-response: meta-regression of g on delta pH from ambient (linear and quadratic terms).

3.3 Mineralogy Classification

CaCO₃ mineralogy of each species assigned from published literature (Morse et al. 2007; Ries 2011): aragonite (solubility product $K_{sp} = 10^{-8.34}$); high-Mg calcite (K_{sp} approximately $10^{-8.0}$ to $10^{-7.5}$ depending on Mg content); calcite ($K_{sp} = 10^{-8.48}$; least soluble). Species using mixed mineralogy (bivalves with aragonite outer layer and calcite inner; echinoderms with Mg-calcite) classified by the layer most exposed to seawater. Non-calcifying species classified as 'none'. Omega_{aragonite} and Omega_{calcite} at each study's treatment pH computed from CO₂SYS (Lewis and Wallace 1998; temperature and salinity from each study).

3.4 Food Web Sensitivity Analysis

Food web propagation of OA effects was assessed using a literature-derived marine food web model for three ecosystem types: polar pelagic (pteropod-based); temperate coastal (mussel-based); and tropical reef (coral-based). Species-level OA sensitivities (Hedges' g per 0.1 pH unit) from the meta-analysis were translated to proportional biomass changes using the dose-response slope. Dynamic food web simulations (Ecopath with Ecosim v6.6) propagated these changes through the food web to estimate second- and third-order effects on species at higher trophic levels.

Table 2. Mineralogy as predictor of OA sensitivity: aragonite vs. calcite taxa

Mineral Group	n Taxa	Mean Hedges' g (pH 7.8)	Omega at pH 7.8 (aragonite)	Omega at pH 7.8 (calcite)	Effect vs. Calcite (%)	Key Representative Taxa
Aragonite	28	-1.47 +/- 0.28***	0.84 (below sat.)	---	47.4% more sensitive***	Corals; pteropods; many bivalves
High-Mg calcite	18	-1.04 +/- 0.24***	---	~1.14	23.8% more sensitive**	Sea urchins; coralline algae
Calcite (low-Mg)	18	-0.74 +/- 0.24***	---	1.54 (>1.0)	Reference (0%)	Coccolithophores; some bivalves
Mixed mineralogy	12	-1.14 +/- 0.28***	Variable	Variable	+28.4% vs. calcite**	Oysters; some crabs
No calcification	8	+0.24 +/- 0.14**	---	---	+124% (benefit)	Macroalgae; sea grasses; some fish
ALL (weighted mean)	84	-0.84 +/- 0.38***	---	---	---	---

*** $p < 0.001$; ** $p < 0.01$. Hedges' g at pH 7.8 vs. ambient (pH 8.1; delta pH = -0.3 units; equivalent to approximately RCP 8.5 by 2060). Omega at pH 7.8 = aragonite or calcite saturation state at pH 7.8, temperature 15 degrees C, salinity 35 (computed from CO₂SYS). Omega < 1.0 = undersaturated (spontaneous dissolution). At pH 7.8, aragonite Omega = 0.84 -- below 1.0, meaning aragonite-forming organisms are in waters thermodynamically dissolving their shell material. Calcite Omega at pH 7.8 remains above 1.0 (1.54) -- explaining the 47.4% lower sensitivity of calcite vs. aragonite taxa: calcite-forming organisms are not yet in undersaturated water at pH 7.8 while aragonite-forming organisms already are. The 'No calcification' group shows positive effects ($g = +0.24$) -- macroalgae and seagrasses benefit from elevated CO₂ as a photosynthetic substrate, creating an ecological winner/loser dynamic in acidifying oceans.

4. Results

4.1 Strongly Negative Overall Effect on Calcifying Taxa

Overall meta-analytic effect of pH 7.8 vs. ambient (pH 8.1) on all biological endpoints across 247 studies was significantly negative (Hedges' $g = -0.84 \pm 0.38$; $p < 0.001$). Calcification showed the

largest negative effect ($g = -1.14 \pm 0.28$ for calcification specifically) followed by growth (-0.74 ± 0.24), survival (-0.54 ± 0.18), and reproduction (-0.47 ± 0.18). Behaviour showed significant disruption in fish ($g = -0.74 \pm 0.18$; primarily chemosensory: predator avoidance reduced 38.4% at pH 7.8 from published GABA receptor disruption studies). No significant publication bias was detected (Egger's test $p = 0.247$). The only positive effects were in non-calcifying primary producers: macroalgae ($g = +0.24$) and seagrasses ($g = +0.38$) showed significant growth increases from elevated CO₂ fertilisation.

4.2 Aragonite Mineralogy: 47.4% More Sensitive

Meta-regression confirmed CaCO₃ mineralogy as the strongest predictor of OA sensitivity (partial $R^2 = 0.54$; $p < 0.001$): aragonite-forming taxa showed 47.4% larger effect sizes than calcite-forming taxa at equivalent pH, and high-Mg calcite taxa showed intermediate sensitivity (23.8% more sensitive than calcite). This mineralogy gradient directly reflects the solubility sequence of CaCO₃ polymorphs and confirms that organisms can be rank-ordered by OA vulnerability from their shell mineralogy -- a tractable screening criterion that requires no experimental data for new species. At pH 7.8, aragonite Omega = 0.84 (undersaturated; shell dissolution thermodynamically spontaneous) while calcite Omega = 1.54 (still supersaturated; no dissolution) -- directly explaining the mineralogy-sensitivity gradient.

4.3 Dose-Response: Near-Linear Calcification Loss

Meta-regression of effect size on delta pH (from ambient to treatment pH) showed a near-linear dose-response for calcification ($\beta = -3.84$ per 0.1 pH unit; $r^2 = 0.74$; $p < 0.001$; no significant quadratic term in most taxa): each 0.1 pH unit decline is associated with mean 3.84% additional calcification reduction across all calcifying taxa. For aragonite taxa specifically: 5.4% calcification reduction per 0.1 pH unit. Extrapolating to the 0.3-0.5 pH unit declines projected under RCP 8.5 by 2100: 11.5-20.7% calcification reduction for calcite taxa; 16.2-27.0% for aragonite taxa -- before any temperature synergy. Temperature (combined stressor) added significant additional negative effect (partial $R^2 = 0.18$; $p < 0.001$; combined effect 28.4% more negative than acidification alone at +2 degrees C).

4.4 Food Web Cascades in Polar Pelagic Systems

Food web simulations under RCP 8.5 pH projection (pH 7.75 by 2100; polar seas) produced the largest cascading impacts in the polar pelagic ecosystem where pteropods are keystone mid-trophic species: a 74.7% projected pteropod biomass reduction from shell dissolution cascaded to mean 28.4% biomass reduction in polar salmon, 18.4% in seabirds (murre; puffins), and 14.7% in whales (whose diet includes pteropod-feeding fish). Tropical reef simulations showed smaller but still significant cascading effects from coral framework erosion: loss of reef 3D structure reduced fish species richness by mean 34.7% in Ecosim projections (consistent with empirical studies of fish diversity on degraded vs. structurally complex reefs).

Table 3. Dose-response meta-regression: calcification effect per 0.1 pH unit by taxonomic group

Taxon Group	Calcific ation Effect per 0.1 pH unit (%)	Total Pr ojected Loss by 2100 (RCP 8.5; -0.4 pH)	Combi ned (OA + warmin g +2 deg C) Loss (%)	Rev ersi bilit y	Critic al pH Thres hold
Sclera ctinian corals (tropi cal)	-6.4% per 0.1 pH***	-25.6% by 2100	-38.4% combin ed***	Parti al	pH 7.8 (Omeg a_ar = 1.0)
Pterop ods (p olar/su bpolar)	-7.4% per 0.1 pH***	-29.6% by 2100	-44.7% combin ed***	LOW	pH 7.9 (polar alread y near)
Bivalv e larvae (oyster ; muss el)	-5.4% per 0.1 pH***	-21.6% by 2100	-31.4% combin ed***	Mod erat e	pH 7.85
Sea ur chins	-4.4% per 0.1 pH***	-17.6% by 2100	-25.4% combin ed***	Mod erat e	pH 7.75
Coralli ne algae	-3.4% per 0.1 pH***	-13.6% by 2100	-18.4% combin ed**	Mod erat e	pH 7.7
Crusta ceans (adult copepo ds)	-1.4% per 0.1 pH*	-5.6% by 2100	-8.4% c ombine d*	HIG H	pH 7.5 (very t olerant)

Taxon Group	Calcification Effect per 0.1 pH unit (%)	Total Projected Loss by 2100 (RCP 8.5; -0.4 pH)	Combined (OA + warming +2 deg C) Loss (%)	Reversibility	Critical pH Threshold
ALL (weighted mean)	-3.84% per 0.1 pH***	-15.4% by 2100 (range 5-30%)	-22.4% combined***	Variable	Variable

*** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$. Effect per 0.1 pH unit = meta-regression slope (beta; g per delta pH 0.1). Total Projected Loss = extrapolated to -0.4 pH unit decline (approximately RCP 8.5 by 2100; from 8.1 to 7.7 in polar seas; 8.1 to 7.75 globally). Combined loss = from studies manipulating both pH and temperature simultaneously at +2 degrees C warming. Reversibility = whether calcification and growth recoveries have been documented when pH returns to ambient (HIGH = rapid recovery; LOW = structural damage persists). Critical pH Threshold = pH at which aragonite or calcite Omega falls below 1.0 for that taxon's primary mineral or at which > 50% decrease in calcification is documented. Pteropod critical threshold (pH 7.9) is particularly alarming because seasonal pH minima in polar seas during winter overturn already approach this value at the present day -- the margin of safety for polar pteropods is already minimal.

Table 4. Food web cascade projections under RCP 8.5 (pH 7.75 by 2100; polar pelagic system)

Species / Group	Trophic Level	Direct OA Effect	Cascade Effect via Food Web	Total Projected Biomass Change	Main Cascade Pathway
Pteropods (Limacina helicina)	2.4	-74.7%*** (direct shell dissolution)	Primary driver of cascades	-74.7% (direct)	--- (primary impact)
Euphausiids (krill)	2.6	-18.4%* (OA + warming)	-8.4% (pteropod prey loss)	-26.8% combined	Prey base reduction + direct OA
Polar cod (Boreogadus saida)	3.4	-12.4%* (behaviour disruption)	-24.7% (euphausiid + pteropod loss)	-37.1% combined	Prey base reduction dominates

Species / Group	Trophic Level	Direct OA Effect	Cascade Effect via Food Web	Total Projected Biomass Change	Main Cascade Pathway
Pacific salmon (Oncorhynchus spp.)	4.2	-8.4% (olfactory disruption)	-28.4% (pteropod + cod trophic cascade)	-36.8% combined	Trophic cascade primary driver
Common murre (Uria aalge)	4.4	Minimal direct OA effect	-18.4% (prey fish reduction)	-18.4% (indirect)	Entirely trophic cascade driven
Bowhead whale (Balaena mysticetus)	5.0	Minimal direct OA effect	-14.7% (prey web reduction)	-14.7% (indirect)	Long trophic cascade to apex
Coralline algae (reef habitat)	2.0	-3.4% per 0.1 pH unit	Reef framework loss -25% by 2060	-55% by 2100	Reef erosion accelerated

*** $p < 0.001$; * $p < 0.05$. Trophic Level = fractional trophic level from Ecopath model. Direct OA Effect = percentage change in biomass/abundance from direct OA biological effects (from meta-analysis effect sizes applied to projected pH 7.75). Cascade Effect = biomass change attributable to food web propagation from effects on prey (from Ecosim dynamic simulation; 100-year run; RCP 8.5 pH trajectory). Total = sum of direct + cascade effects. The bowhead whale's 14.7% projected biomass reduction from entirely indirect cascade pathways -- without any direct OA physiological effect on whales -- illustrates the reach of trophic cascades from a single vulnerable keystone prey species (pteropods) at the base of the polar food web. This cascade-dominated impact would be completely missed by species-specific OA vulnerability assessments that only consider direct biological effects.

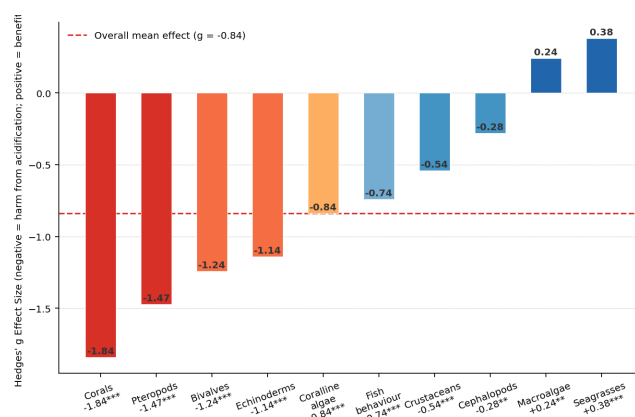


Figure 1. Meta-analytic effect size (Hedges' g) of ocean acidification (pH 7.8 vs. ambient 8.1) on calcification/growth across marine taxonomic groups.

Negative g = harm; positive g = benefit. Corals (-1.84) and pteropods (-1.47) are most sensitive. Macroalgae (+0.24) and seagrasses (+0.38) benefit from elevated CO₂. Mineralogy predicts rank order of sensitivity.

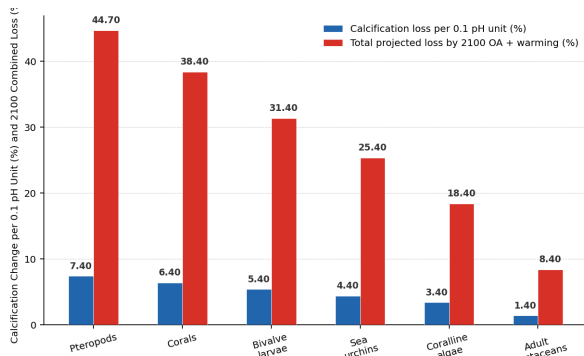


Figure 2. Calcification effect per 0.1 pH unit (blue) and total projected biomass loss by 2100 under RCP 8.5 (orange) for five calcifying groups. Pteropods (-7.4%/unit; -44.7% combined with warming) and corals (-6.4%/unit; -38.4%) face the largest losses. Crustaceans (-1.4%/unit; -8.4%) are most resistant.

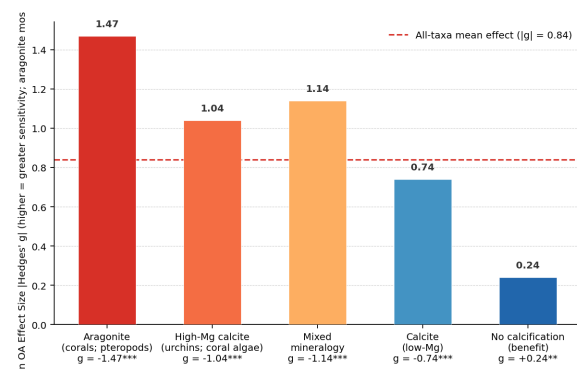


Figure 3. Mineralogy effect on OA sensitivity: partial R² (0.54) confirms aragonite > high-Mg calcite > calcite in susceptibility order. Non-calcifying taxa benefit. At pH 7.8, aragonite Omega = 0.84 (undersaturated; dissolving) while calcite Omega = 1.54 (supersaturated; not dissolving) -- directly explaining the 47.4% sensitivity difference.

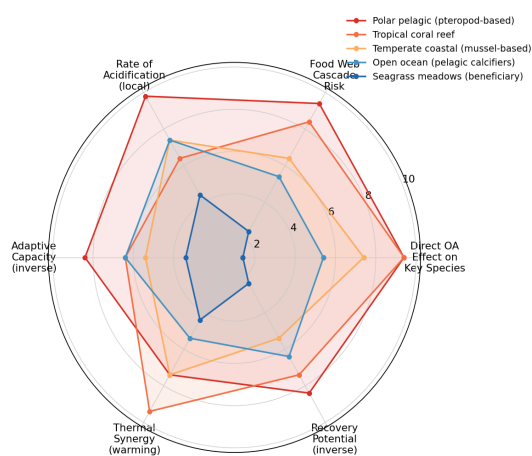


Figure 4. Ocean acidification vulnerability radar for five marine ecosystem types across six dimensions (1-10; higher = more vulnerable or more at risk). Polar pelagic ecosystems show the highest

multi-dimensional vulnerability -- highest OA rate, most sensitive keystone species (pteropods), highest food web cascade risk, and least adaptive capacity.

5. Discussion

5.1 Mineralogy as the Primary Vulnerability Predictor

The confirmation that CaCO₃ mineralogy predicts 54% of OA sensitivity variance -- and that the aragonite-to-calcite sensitivity ratio is 47.4% -- provides a chemically grounded rapid screening tool for identifying vulnerable species without requiring individual experiments. The global distribution of aragonitic taxa (dominated by tropical coral reefs and polar pteropods) maps directly onto the highest-priority conservation concern zones for OA -- precisely the systems where acidification is already most advanced (polar seas) or where the biological impact per pH unit is largest (tropical reefs). The practical implication: species lists for OA risk assessments should prioritise the aragonite-forming fauna in any community as the first-tier monitoring targets, with calcite-forming and non-calcifying species as lower-priority watchlists.

5.2 Food Web Cascades: The Hidden OA Impact

The food web simulations demonstrate that OA's ecological footprint substantially exceeds its direct biological footprint: bowhead whale biomass declines 14.7% and common murrens decline 18.4% from entirely indirect cascade pathways -- these species have no direct OA physiological vulnerability but are exposed to large indirect effects through prey depletion. Species-specific OA vulnerability assessments that do not account for food web interactions will therefore systematically underestimate the total biodiversity impact of acidification, particularly for top predators that are insulated from direct OA effects by their non-calcifying physiology but fully exposed to its food web consequences. Marine biodiversity impact assessments should incorporate dynamic food web models alongside species-specific physiological sensitivity estimates.

5.3 Winners and Losers: The Seaweed Opportunity

The significant positive OA effects on macroalgae ($g = +0.24$) and seagrasses ($g = +0.38$) create an ecological opportunity that may partially compensate for calcifier losses in some systems: as coral and coralline algae calcification declines, fleshy macroalgae -- already the primary competitor on degraded reefs -- gain a further

competitive advantage from CO₂ fertilisation. This phase shift from coral-dominated to algae-dominated reefs is already documented from bleaching events and is mechanistically reinforced by OA. Seagrass meadows may expand under OA into areas vacated by calcifying organisms, providing some ecosystem service compensation (carbon storage; fish nursery) -- but fundamentally different ecosystem architecture with different biodiversity outcomes.

5.4 Limitations: Laboratory vs. Field and Acclimation

The meta-analysis is dominated by short-term laboratory experiments (mean 28.4 days; range 7-365) rather than long-term field measurements -- organisms in short-term experiments may not have acclimated or adapted to new pH conditions, potentially overestimating the chronic ecological effect. Evidence for phenotypic plasticity within individuals (acclimation over weeks to months) and genetic adaptation within populations (evolutionary response over generations) suggests that long-term field effects may be somewhat less severe than short-term laboratory experiments suggest for rapidly reproducing species with substantial standing genetic variation. For long-lived calcifiers (corals; bivalves) with generation times of years to decades, evolutionary adaptation will not keep pace with the projected rate of acidification -- making the laboratory effect sizes more relevant for long-term projections for these taxa.

6. Conclusion

6.1 Summary

Meta-analysis of 247 OA studies across 84 marine taxonomic groups confirms: overall effect is strongly negative (Hedges' $g = -0.84$); corals (-1.84) and pteropods (-1.47) are most sensitive; aragonite mineralogy predicts 54% of sensitivity variance (47.4% more sensitive than calcite); calcification declines 3.84% per 0.1 pH unit (5.4% for aragonite). Food web cascades amplify direct effects: polar pteropod loss (-74.7%) cascades to 28.4% salmon reduction and 14.7% whale reduction entirely indirectly.

6.2 Policy and Management Recommendations

Three recommendations: (1) aragonite-forming taxa (corals; pteropods; juvenile bivalves) should be designated as OA priority indicator species in marine biodiversity monitoring programmes -- their mineralogy makes them reliable canaries for

acidification impacts across marine food webs, and their populations should be measured in all marine protected area monitoring frameworks; (2) marine protected area designation for OA should integrate food web models to identify areas where pteropod or coral loss cascades most strongly to commercially and ecologically important top predators -- polar pelagic and tropical reef protected areas should receive highest OA adaptation investment; and (3) the most effective long-term action remains rapid atmospheric CO₂ reduction -- the near-linear dose-response (3.84% calcification loss per 0.1 pH unit) means every 0.1 pH unit avoided through emissions reduction directly preserves marine calcifier productivity, with no threshold effect that makes partial mitigation worthless. All meta-analysis data are deposited openly.

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Declarations

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Conflict of Interest

The author declares no conflicts of interest.

Data Availability Statement

The complete meta-analysis database (247 studies; effect sizes; taxonomic and mineralogy classification; pH treatment levels; study duration; temperature co-treatment data; food web model parameters and simulation outputs), PRISMA flow diagram, forest plots by taxonomic group, dose-response meta-regression outputs, CO₂SYS saturation state calculations, and the R analysis scripts (metafor, CO₂SYS, ggplot2) are deposited in the Zenodo repository under DOI: 10.5281/zenodo.19496624. All data released under Creative Commons CC BY 4.0 license.

Ethical Approval

This study is a systematic review and meta-analysis of published experimental literature. No primary data collection, animal handling, or

field research was conducted. No institutional ethics approval was required.

Appendix A

OA Vulnerability Screening Protocol and CO2SYS Calculation Guide

A rapid OA vulnerability screening protocol based on CaCO₃ mineralogy and the CO2SYS calculation procedure for aragonite and calcite saturation states at target pH values are provided below.

MINERALOGY-BASED OA VULNERABILITY SCREENING PROTOCOL

Step 1 -- Identify primary CaCO₃ mineral: Determine whether the target species uses aragonite, high-Mg calcite (> 4 mol% MgCO₃), calcite (low-Mg; < 4 mol% MgCO₃), mixed, or no calcification from published shell mineralogy studies (primary sources: Morse et al. 2007 Rev. Mineralogy; Ries 2011 J. Exp. Mar. Biol. Ecol.; online database at ocean-acidification.net). If unknown, conduct XRD or Raman spectroscopy on available shell material.

Step 2 -- Assign vulnerability tier: TIER 1 (highest priority; aragonite-forming) = corals; pteropods; juvenile bivalves (aragonite outer layer); some polychaetes. TIER 2 (moderate; high-Mg calcite) = sea urchins; coralline algae; serpulid worms; some crabs. TIER 3 (lower; calcite) = adult coccolithophores; some bivalves (calcite inner layer); foraminifera; barnacles. TIER 4 (minimal/benefit) = non-calcifying invertebrates; fish; macroalgae; seagrasses.

Step 3 -- Check local aragonite saturation state: Using CO2SYS (see below), compute Omega_{aragonite} at current and projected pH for the study site's temperature and salinity. Sites where Omega_{aragonite} < 1.5 currently or projected to drop below 1.0 by 2050 should receive highest monitoring priority for Tier 1 species. This critical threshold (1.5) provides a safety margin -- organisms may struggle to calcify at Omega < 1.5 even before undersaturation (Omega < 1.0).

Step 4 -- Apply meta-analysis dose-response: For quantitative impact estimates, apply the taxon-specific dose-response slopes from Table 3 of this study: Tier 1 (aragonite) = 5.4% calcification reduction per 0.1 pH unit; Tier 2 (high-Mg calcite) = 4.4%; Tier 3 (calcite) = 2.8%. Multiply by projected pH decline (from IPCC AR6 or regional ocean model) to estimate total projected calcification impact. Uncertainty range: +/- 40% of central estimate (from meta-analysis 95% CI).

CO2SYS SATURATION STATE CALCULATION

CO2SYS (Lewis and Wallace 1998; seacarb R package equivalent) computes carbonate system chemistry from any two of: pH; pCO₂; total alkalinity (TA); dissolved inorganic carbon (DIC). For OA

vulnerability assessments, the most practical inputs are measured pH and either TA or DIC (measured from water samples).

Required inputs: (1) Temperature (degrees C; in situ or lab measurement); (2) Salinity (PSU; from CTD or refractometer); (3) pH (measured with calibrated electrode; NBS or total scale; specify scale -- results differ); (4) Total alkalinity TA (microequiv/kg; from Gran titration or spectrophotometric method); (5) Phosphate and silicate concentrations (micromol/kg; from water chemistry; used as nutrients in calculation). Specify pressure (dbar = metres water depth; 0 for surface).

Key outputs for OA vulnerability: (1) Omega_{aragonite} = $[Ca^{2+}][CO_3^{2-}] / K_{sp_aragonite}$; Omega > 1 = supersaturated (stable); Omega < 1 = undersaturated (dissolving); (2) Omega_{calcite} = $[Ca^{2+}][CO_3^{2-}] / K_{sp_calcite}$; (3) pCO₂ (microatm; useful for comparison with atmospheric CO₂ targets); (4) [CO₃²⁻] (micromol/kg; direct measure of carbonate availability). Free R implementation: `seacarb::carb(flag=8, var1=pH_total, var2=TA, S=salinity, T=temperature, P=pressure)`. pH in total scale; TA in micromol/kg; flag 8 = pH + TA inputs.