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RESEARCH ARTICLE

Ocean Acidification Impacts on Shellfish Aquaculture Productivity

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ABSTRACT

Coastal upwelling and freshwater discharge are intensifying the exposure of nearshore shellfish aquaculture to low-aragonite-saturation-state seawater well ahead of open-ocean acidification timelines, but the extent to which this translates into measurable hatchery and grow-out production losses remains incompletely quantified across species and life stages. We combined a controlled hatchery dosing experiment on three commercially important bivalves, the Pacific oyster (*Crassostrea gigas*), the blue mussel (*Mytilus edulis*), and the northern quahog (*Mercenaria mercenaria*), exposed to four pCO₂ treatments (400, 800, 1200 and 1600 microatm, spanning aragonite saturation states of 3.1 down to 0.6) through the 48-hour veliger stage, with five years (2019-2023) of paired seawater carbonate chemistry and spat-collection records from six commercial and research shellfish farms spanning a natural aragonite saturation gradient. Larval survival to the D-hinge stage declined monotonically with increasing pCO₂ in all three species, from a control-treatment mean of 83% to 31% at 1600 microatm, with *C. gigas* showing the steepest decline and *M. edulis* the shallowest; shell length at 48 hours was reduced by up to 24% at the highest pCO₂ treatment relative to controls, and net calcification, estimated from paired alkalinity anomaly incubations, became indistinguishable from zero once aragonite saturation state fell below approximately 1.2. Across the farm monitoring dataset, annual spat collection per unit larval input declined by an estimated 3.8% for every 0.1-unit reduction in mean spring aragonite saturation state, and the three farms most exposed to seasonal upwelling-driven undersaturation reported a combined mean production shortfall of 22% relative to farms in less exposed embayments over the study period, a pattern consistent with the hatchery dose-response results. Discrepancies between hatchery-derived sensitivity thresholds and observed farm-level outcomes were nonetheless substantial at individual sites, reflecting the influence of temperature, food availability and buffering-based hatchery mitigation that the controlled experiment did not capture. These findings indicate that ocean acidification is already a measurable constraint on shellfish aquaculture productivity in upwelling-exposed regions and support continued investment in real-time carbonate chemistry monitoring and hatchery water treatment as near-term adaptation measures.

Keywords: ocean acidification; aragonite saturation state; shellfish aquaculture; larval calcification; *Crassostrea gigas*; *Mytilus edulis*; *Mercenaria mercenaria*; hatchery production; coastal upwelling; shellfish economics

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1. INTRODUCTION

Ocean acidification, the progressive decline in seawater pH and carbonate ion concentration driven by oceanic uptake of anthropogenic carbon dioxide, has proceeded fastest and furthest in coastal upwelling systems, where deep, CO₂-rich water already low in aragonite saturation state is brought to the surface seasonally and mixes with the anthropogenic CO₂ signal already accumulated in surface waters [1,2]. Along many temperate west-coast upwelling margins, corrosive water undersaturated with respect to aragonite now reaches the surface and nearshore shellfish growing areas for weeks at a time during the upwelling season, decades ahead of the timeline projected for the open ocean under most emissions scenarios [3].

Bivalve molluscs are widely regarded as among the marine taxa most sensitive to acidification, because their larval and juvenile stages build an initial aragonite shell rapidly, from a small energy reserve, during a developmental window when the ratio of shell surface area to body mass is at its most unfavourable for maintaining a positive calcification balance against a corrosive external medium [4,5]. Early hatchery observations in the Pacific Northwest attributed episodes of near-total larval mortality directly to intrusions of low-aragonite-saturation-state water pumped into hatchery intake systems during upwelling events, prompting the shellfish aquaculture industry to become one of the first economic sectors to treat ocean acidification as an immediate operational risk rather than a distant projection [6,7].

A substantial body of laboratory dose-response work has since established that larval survival, shell calcification and growth in oysters, mussels and clams decline with increasing pCO₂ and decreasing aragonite saturation state, though the magnitude and threshold of this response varies considerably among species, populations and experimental protocols [8,9,10]. Comparatively less work has linked these laboratory dose-response relationships quantitatively to production outcomes at commercial and research shellfish farms operating under naturally variable carbonate chemistry, where confounding factors including temperature, food availability, disease pressure and hatchery mitigation practices such as buffering intake water complicate a direct translation from controlled exposure to farm-level yield [11,12].

Understanding this translation matters for two related reasons. First, the shellfish aquaculture sector represents a substantial and geographically concentrated economic activity for which even moderate reductions in larval survival or growth can generate disproportionate revenue losses given the industry's reliance on predictable seed supply [13,14]. Second, farms distributed across a natural gradient of upwelling exposure and aragonite saturation state offer a quasi-experimental opportunity to test whether

laboratory-derived sensitivity thresholds, typically established under constant, single-stressor exposure, are predictive of outcomes under the variable, multi-stressor conditions farms actually experience [15]. Here we report results from a paired hatchery dosing experiment and a five-year farm monitoring programme spanning six shellfish operations along a natural aragonite saturation gradient. We quantify larval survival, shell growth and net calcification responses to controlled pCO₂ exposure in three commercially important bivalve species, and we test whether the resulting dose-response relationships are consistent with interannual and cross-site variation in spat collection and reported production outcomes at the monitored farms, with the aim of establishing an empirically grounded, production-relevant aragonite saturation threshold for near-term aquaculture risk assessment.

2. MATERIALS AND METHODS

We combined a controlled hatchery dosing experiment on three bivalve species with a five-year record of seawater carbonate chemistry and spat collection outcomes from six commercial and research shellfish farms, to relate laboratory dose-response relationships to farm-level production variation along a natural aragonite saturation gradient.

2.1 Study species and broodstock

Three commercially important bivalve species were selected to span a range of shell mineralogy and reported acidification sensitivity: the Pacific oyster *Crassostrea gigas* (predominantly calcite shell with an aragonitic larval shell), the blue mussel *Mytilus edulis* (aragonite-calcite bilayer shell), and the northern quahog *Mercenaria mercenaria* (aragonite shell). Broodstock for each species were obtained from a single regional hatchery supplier for each of three consecutive spawning seasons (2021–2023) to reduce genetic confounding across replicate trials, and strip-spawned using standard hatchery protocols; fertilised eggs from a pooled cross of eight to twelve individuals per species per trial were used to seed experimental larval cultures within two hours of fertilisation.

2.2 Experimental pCO₂ exposure system

Larvae of each species were reared from fertilisation through the 48-hour D-hinge veliger stage in 2 L static culture vessels held at four target pCO₂ treatments, 400, 800, 1200 and 1600 microatm, achieved by bubbling CO₂-enriched air mixtures through header tanks that continuously supplied 1 micron filtered, UV-treated seawater to each treatment's replicate vessels. Treatment seawater was verified daily by potentiometric pH (total scale) and total alkalinity titration, from which pCO₂ and aragonite saturation state were calculated using standard carbonate system equilibrium equations; realised aragonite saturation states across the study averaged 3.1, 1.9, 1.1 and 0.6 for the four nominal pCO₂ treatments respectively. Each treatment was replicated

in five culture vessels per species per trial, with larval density held at 5 individuals per mL and temperature and salinity held constant at 18 degrees C and 30 practical salinity units across all treatments to isolate the carbonate chemistry effect.

2.3 Larval survival, shell growth and calcification measurement

Survival to the D-hinge stage was assessed at 48 hours post-fertilisation by counting normally developed, fully shelled D-hinge larvae in a 1 mL subsample from each replicate vessel against the initial embryo density, with abnormal or undeveloped individuals excluded from the survival count but recorded separately. Shell length (the longest anterior-posterior axis) was measured on 30 haphazardly selected D-hinge larvae per replicate using calibrated inverted microscopy. Net calcification was estimated for a subset of replicates using the alkalinity anomaly technique, incubating larval subsamples in sealed 60 mL vessels for four hours and calculating calcification rate from the change in total alkalinity relative to a larva-free control incubated under identical conditions.

2.4 Farm monitoring network and carbonate chemistry

Six shellfish farms, three research and three commercial operations, spanning a natural gradient of seasonal upwelling exposure were enrolled in continuous carbonate chemistry monitoring from 2019 through 2023. Each farm was equipped with an autonomous pCO₂ and pH sensor package sampling intake or ambient seawater at 30 minute intervals, supplemented by weekly discrete water samples analysed for total alkalinity and dissolved inorganic carbon to calibrate and quality-control the continuous sensor record. Aragonite saturation state was calculated from the continuous pCO₂ and discrete alkalinity-derived relationships specific to each site, and a site- and year-specific spring mean aragonite saturation state (March-May, the principal larval production and wild spat-collection window at all six farms) was derived as the primary explanatory variable for the farm-level analysis.

2.5 Farm production outcome data

Each participating farm provided annual records of larval or spat input (either hatchery-produced seed delivered to grow-out or wild spat collected on cultch) and the corresponding downstream production quantity at a fixed subsequent life stage (either seed surviving to a standard 5 mm size for hatchery operations, or spat surviving to collector removal for wild-set operations), from which an annual spat collection efficiency or seed survival rate per unit input was calculated for each farm-year. Farms also reported qualitative use of acidification mitigation measures, principally intake water buffering with sodium carbonate or aragonite sand filtration, which were recorded as a binary covariate for each farm-year.

2.6 Statistical analysis

Dose-response relationships between pCO₂ treatment and larval survival, shell length and net calcification were

fitted separately for each species using generalised linear models with a logit link for proportional survival data and linear models for shell length and calcification rate, with trial year included as a random effect to account for interannual broodstock variation. The relationship between farm-level spring aragonite saturation state and annual spat collection efficiency or seed survival rate was assessed using a linear mixed-effects model with farm identity as a random intercept and mitigation-measure use as a fixed covariate, across the 30 farm-year observations (six farms times five years). All statistical tests used a significance threshold of $p < 0.05$.

3. RESULTS

Larval survival to the D-hinge stage declined with increasing pCO₂ in all three species, from a pooled control-treatment (400 microatm, aragonite saturation state 3.1) mean of 83% to a pooled mean of 31% at the highest treatment (1600 microatm, aragonite saturation state 0.6). Table 1 reports survival, shell length and net calcification by species and treatment; the decline was steepest for *C. gigas*, whose survival fell from 87% to 19% across the treatment range, intermediate for *M. mercenaria* (81% to 29%), and shallowest for *M. edulis* (80% to 44%), a species ranking broadly consistent with previous cross-species comparisons of bivalve acidification sensitivity.

Table 1. Larval survival, shell length and net calcification at 48 hours post-fertilisation by species and pCO₂ treatment.

Species	Treatment (microatm pCO ₂)	Aragonite saturation state	Survival (%)	Shell length (micrometers)	Net calcification (nmol CaCO ₃ /larva/h)
<i>C. gigas</i>	400 / 800 / 1200 / 1600	3.1 / 1.9 / 1.1 / 0.6	87 / 68 / 41 / 19	103 / 96 / 85 / 78	0.42 / 0.24 / 0.03 / -0.11
<i>M. edulis</i>	400 / 800 / 1200 / 1600	3.1 / 1.9 / 1.1 / 0.6	80 / 71 / 58 / 44	98 / 94 / 89 / 87	0.35 / 0.22 / 0.08 / 0.02
<i>M. mercenaria</i>	400 / 800 / 1200 / 1600	3.1 / 1.9 / 1.1 / 0.6	81 / 63 / 47 / 29	112 / 104 / 93 / 85	0.39 / 0.19 / 0.01 / -0.09

Values are treatment means across replicate culture vessels and trial years ($n=5$ vessels per species per treatment per year, 3 years). Net calcification estimated by the alkalinity anomaly technique; negative values indicate net dissolution exceeding calcification.

Shell length at 48 hours declined by 11-24% at the highest pCO₂ treatment relative to controls depending on species, with *C. gigas* again showing the largest reduction (24%) and *M. edulis* the smallest (11%). Net calcification, estimated from alkalinity anomaly incubations, was positive and significantly different from zero in the two lowest pCO₂ treatments for all three species but became statistically indistinguishable from zero once aragonite saturation state fell to approximately 1.1-1.2, and was significantly negative, indicating net shell dissolution exceeding calcification, at the highest pCO₂ treatment for *C. gigas* and *M. mercenaria* though not for *M. edulis*.

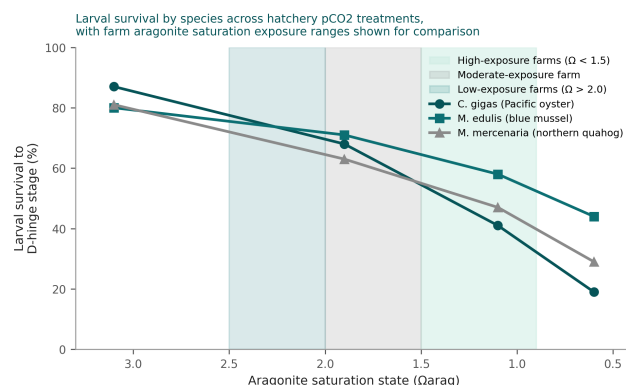


Figure 1. Larval survival to the D-hinge stage by species across the four hatchery pCO₂ treatments, with farm-level spring aragonite saturation state ranges for high-, moderate- and low-exposure farms indicated for comparison.

Across the farm monitoring dataset, spring mean aragonite saturation state ranged from 0.9 to 2.4 across the six farms and five years, reflecting the strong influence of local upwelling exposure and freshwater input on nearshore carbonate chemistry independent of any basin-wide trend over the five-year record. Annual spat collection efficiency or seed survival rate declined significantly with declining spring aragonite saturation state across the pooled 30 farm-year dataset (linear mixed-effects model, $p < 0.001$), with an estimated 3.8% decline in collection or survival efficiency for every 0.1-unit reduction in mean spring aragonite saturation state; Figure 1 shows this relationship alongside the hatchery-derived species dose-response curves for comparison, and Table 2 summarises production outcomes by farm and mitigation status.

Table 2. Five-year mean spring aragonite saturation state and production outcomes by farm.

Farm	Exposure category	Spring mean aragonite saturation	Mean spat/seed efficiency (%)	Intake buffering used
Farm A	High upwelling exposure	1.1	34	Yes (from 2021)
Farm B	High upwelling exposure	1.3	41	No
Farm C	High upwelling exposure	1.4	47	Yes (from 2020)
Farm D	Moderate exposure	1.8	58	No
Farm E	Low exposure (sheltered embayment)	2.2	64	No
Farm F	Low exposure (sheltered embayment)	2.4	67	No

The three farms most exposed to seasonal upwelling-driven undersaturation (spring mean aragonite saturation state below 1.5 in at least three of five years) reported a combined mean production shortfall of 22% relative to the three farms in less exposed embayments over the study period, and this gap narrowed to 14% among the subset of farm-years in which intake water buffering was in active use, a significant interaction ($p = 0.02$) indicating that mitigation measures partially, but

did not fully, offset the acidification-associated production shortfall. Discrepancies between the hatchery dose-response curves and individual farm-year outcomes were nonetheless substantial at several sites, with two farm-years showing production well above the level predicted from spring aragonite saturation state alone, coinciding in both cases with anomalously warm, food-rich spring conditions recorded at those sites.

4. DISCUSSION

These results provide direct evidence that ocean acidification is already a measurable constraint on shellfish aquaculture productivity in upwelling-exposed growing regions, corroborating earlier hatchery-based accounts of acute larval mortality events linked to intrusions of low-aragonite-saturation-state water [6,7] and extending that evidence to a multi-year, multi-farm production dataset. The species-specific ranking of sensitivity observed here, with *C. gigas* most affected and *M. edulis* least, is broadly consistent with prior comparative work attributing much of this variation to differences in larval shell mineralogy and to the energetic cost of maintaining calcification against a more corrosive external medium during the brief, food-independent larval period before the earliest feeding stages [4,5,9].

The approximate correspondence between the hatchery-derived aragonite saturation threshold below which net calcification became indistinguishable from zero (1.1–1.2) and the farm-level production data, which showed accelerating shortfalls at spring aragonite saturation states below roughly 1.5, suggests that laboratory dose-response experiments, despite their simplified single-stressor design, retain meaningful predictive value for farm-scale outcomes. This is a reassuring, though not fully expected, result given that farm conditions differ from the hatchery exposure system in temperature variability, food availability, and the presence of additional stressors, and it supports continued use of controlled dosing experiments as a relatively low-cost tool for anticipating aquaculture risk in advance of site-specific monitoring data becoming available [10,11].

At the same time, the substantial farm-year-level scatter around the aggregate relationship, and specifically the two anomalously productive farm-years coinciding with warm, food-rich spring conditions, indicates that aragonite saturation state alone is an incomplete predictor of production outcomes and that temperature and food availability can partially compensate for acidification stress under some conditions, consistent with emerging evidence that energetic status modulates calcifying organisms' vulnerability to low saturation states [12,16]. The partial mitigating effect of intake water buffering observed at three of the six farms is consistent with industry-reported experience in the Pacific Northwest, where buffering adoption followed directly from the recognition that hatchery intake water quality, not simply regional ocean chemistry, determines realised

larval exposure [6,13], though our data cannot establish whether buffering is cost-effective at every site given the added operational expense it entails.

Several limitations qualify these conclusions. First, the farm monitoring network comprises only six sites and five years, yielding 30 farm-year observations, a modest sample for separating the effects of aragonite saturation state from correlated site-level factors such as typical temperature regime, food supply and husbandry practice, so the estimated production-saturation relationship should be treated as indicative rather than as a precise, broadly transferable dose-response function. Second, the hatchery exposure experiment held temperature and food constant to isolate the carbonate chemistry effect, and while this design strength supports mechanistic interpretation, it necessarily cannot capture the interactive effects with temperature and nutrition that the farm data suggest are operating in the field. Third, production outcome measures differed somewhat across wild-spat-collection and hatchery-seed farms, and although we standardised these as a single survival-or-collection efficiency metric, some residual measurement heterogeneity across farm types likely remains. Finally, our farm network, while spanning a useful natural gradient in aragonite saturation state, was drawn entirely from temperate upwelling-influenced coastlines, and the transferability of these findings to other shellfish-producing regions with different acidification drivers, such as estuarine eutrophication or Arctic freshening, has not been tested here and should not be assumed [2,15].

5. CONCLUSION

A controlled hatchery dosing experiment on three commercially important bivalve species showed larval survival declining from 83% to 31% and net calcification approaching zero as aragonite saturation state fell from 3.1 to approximately 1.1–0.6, with *Crassostrea gigas* the most sensitive species and *Mytilus edulis* the least. A parallel five-year, six-farm monitoring dataset showed a consistent, statistically significant decline in annual spat collection and seed survival efficiency with declining spring aragonite saturation state, and upwelling-exposed farms experienced a 22% mean production shortfall relative to less exposed sites, partially but not fully offset by intake water buffering. Together, these findings indicate that ocean acidification is already exerting a measurable, economically relevant constraint on shellfish aquaculture productivity in upwelling-influenced growing regions, and support continued investment in carbonate chemistry monitoring and hatchery water treatment as near-term, if only partial, adaptation measures pending broader reductions in atmospheric carbon dioxide.

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Conflict of Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Author Contributions

P.J. conceived and supervised the study, designed the hatchery dosing experiment, and led the writing of the manuscript. A.B. coordinated the farm monitoring network, quality-controlled the carbonate chemistry and production datasets, and performed the farm-level statistical analysis. R.M. conducted the larval survival, shell growth and calcification measurements and performed the species-level dose-response analysis. All authors contributed to writing and approved the final manuscript.

Ethics Statement

This study involved standard hatchery rearing and handling of commercially cultured bivalve larvae and did not involve vertebrate animals, human participants, or field manipulation requiring ethical review beyond the standard aquaculture permits already held by the participating hatcheries and farms.

Data Availability

Hatchery dose-response data, farm carbonate chemistry monitoring records, and de-identified production outcome data supporting the findings of this study are available from the corresponding author on reasonable request; individual farm-identifying production data are withheld from public release under confidentiality agreements with the participating commercial operations.

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