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Marine Heatwaves Associated with Hypoxia in Coastal Bivalve Aquaculture and Management Implications

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Abstract. Marine heatwaves alter coastal dissolved oxygen dynamics and exacerbate hypoxia risk for farmed bivalves, yet causal relationships between warming and low oxygen remain poorly differentiated in aquaculture assessments. This paper establishes a three-category attribution framework to distinguish hypoxia directly induced by marine heatwaves, background hypoxia amplified during thermal anomalies, and merely coincident high-temperature and low-oxygen events. Compiled physiological and experimental evidence demonstrates that combined heat and hypoxia impose species-specific impacts on feeding, metabolism, antioxidant defence and survival, with nocturnal oxygen minima driving growth losses hidden by daily mean dissolved oxygen values. Molecular stress markers reflect cellular defence activation but cannot reliably predict harvest biomass or economic outcomes. Site characteristics, organismal traits and exposure recurrence modify stress responses, so universal oxygen thresholds are unsuitable for farm risk management. Integrated high-frequency monitoring and targeted aeration can mitigate oxygen-related damage, though thermal injury persists. This synthesis highlights the necessity of site-specific adaptive strategies to improve climate resilience of coastal bivalve aquaculture.

Keywords: Marine heatwaves, coastal hypoxia, dissolved oxygen, bivalve aquaculture, climate-resilient management

1. Introduction

Marine heatwaves (MHWs) are periods of unusually warm seawater relative to a local seasonal baseline. Recent global analysis shows that marine heatwaves increasingly coincide with low-oxygen extremes, while regional seabed analysis demonstrates that warming can reduce oxygen availability in shallow coastal waters [1, 2]. For bivalve aquaculture, the importance of this coupling is practical in real farm operations. Farmed oysters, clams, mussels, and scallops are sessile or semi-sessile, so they cannot readily leave a deteriorating water mass. Many culture sites also retain heat and organic matter, and their animals obtain both oxygen and food by ventilating the surrounding water. Higher temperature can increase maintenance metabolism and oxygen demand, whereas falling DO limits aerobic supply. The biological risk therefore comes from a changing supply and demand balance, not from temperature or DO considered in isolation.

The current evidence base remains uneven. A growing set of environmental studies describes the co-occurrence of warming and oxygen decline, and recent bivalve experiments document strong

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species differences under recurrent heat exposure [1-3]. Direct temperature × DO factorial evidence is still limited compared with single-stressor work. Laboratory experiments can separate temperature effects, DO effects, and statistical interactions, but their fixed levels may simplify natural onset, diel cycling, and recovery. Field observations capture realistic exposure but often do not identify whether an MHW caused a deficit, amplified background hypoxia, or merely coincided with it. Molecular and physiological studies can reveal defence pathways and short-term compensation, yet they do not automatically predict feeding, growth, reproduction, mortality, harvestable biomass, or economic loss. In particular, recurrent night-time oxygen minima may be hidden by daily mean DO. A recent management framework also emphasizes that climate risk cannot be separated from site conditions, production decisions, and the capacity to act on warnings [4].

To fill these research gaps, this review systematically unpacks biogeochemical pathways linking marine heatwaves to coastal oxygen limitation, then evaluates organismal and farm-scale biological consequences. Its core objective is to develop an attribution framework to classify whether observed dissolved oxygen deficits are heatwave-driven, amplified from pre-existing hypoxia, or merely coincident with warming. Evidence from controlled factorial assays, field observations and molecular studies are synthesised to compare inference strength across different research approaches. This analysis traces stress impacts from oxygen supply-demand imbalance to behavioural shifts, metabolic depression, oxidative defence, mortality and potential reproductive costs. Biological traits, thermal acclimation, water exchange, organic loading, stocking density and repeated exposure are treated as key modifiers shaping actual stress intensity experienced by cultured bivalves. The final discussion proposes monitoring schemes, targeted intervention measures and climate-adaptive aquaculture design. Oxygen thresholds are only meaningful when paired with exposure duration, recurrence and recovery dynamics, and statistical interactions between temperature and dissolved oxygen are carefully distinguished from biological synergistic effects.

2. Formation of oxygen limitation associated with marine heatwaves

2.1. Marine heatwaves as an upstream driver of oxygen decline

Temperature changes the coastal oxygen budget through several linked routes. Warm water holds less oxygen at saturation, surface warming can strengthen density gradients and restrict ventilation, and temperature-sensitive respiration by bivalves, microbes, and sediments can increase. Global analysis identifies heatwave-associated low-oxygen extremes [1]. In the Baltic seabed study, events defined by bottom-water temperature of at least 17 °C for at least 10 consecutive days occurred mainly shallower than 20 m; bottom water was 3–10 °C warmer and oxygen differences reached approximately −3 mL L^{-1}, with most of the decline explained by solubility [2]. This supports a regional heat-to-oxygen pathway, not a universal farm-scale threshold. Wind, tides, freshwater input, bathymetry, and exchange can weaken local coupling.

2.2. Background coastal hypoxia and its amplification during warming

Coastal hypoxia can begin before a marine heatwave. Nutrient enrichment and organic matter increase microbial and sediment oxygen demand, while weak exchange, stratification, benthic respiration, and night-time respiration delay oxygen recovery. Farm biodeposition and high stocking biomass may add local oxygen demand, but their contribution varies widely across cultivation sites. A marine heatwave can deepen or prolong this oxygen deficit by lowering saturation, increasing respiration, or shortening reoxygenation windows. Nearshore field observations show that nocturnal

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dissolved oxygen can stay at extremely low levels for multiple consecutive hours, even when daily-averaged dissolved oxygen appears adequate. Field flow-through tests further confirm that daily average values conceal biologically relevant nocturnal hypoxia exposure, which imposes persistent stress on bivalves.

2.3. A three-category attribution framework

The environmental record should distinguish three situations. MHW-induced hypoxia is shown when anomalous warming lowers oxygen through solubility, stratification, reduced ventilation, or enhanced consumption. MHW-amplified pre-existing hypoxia is a background deficit that becomes more severe or persistent during warming. Co-occurring high temperature and low DO describes an overlap for which seasonality, eutrophication, hydrodynamics, and other drivers remain unresolved. The third category is not proof of either pathway. Time-resolved records, oxygen budgets, and an appropriate counterfactual are needed before assigning causation.

2.4. From environmental coupling to oxygen supply and demand imbalance

For a cultured bivalve, the relevant exposure is the balance between oxygen delivered by the water and oxygen required by the animal. Warming can increase maintenance demand before DO changes, creating a direct thermal burden; oxygen decline then reduces external supply. Depending on intensity and recovery, a bivalve may close its valves, reduce pumping, depress metabolism, or recruit anaerobic pathways. These adjustments can delay mortality but reduce energy acquisition. A temperature × DO factorial design estimates main effects and interactions, but does not make temperature and DO independent environmental drivers.

3. Biological responses of farmed bivalves to oxygen limitation associated with marine heatwaves

3.1. Direct evidence for metabolic and behavioural adjustment

Matched temperature and DO treatments provide the clearest evidence for compound exposure. In adult northern bay scallops, 29.0 ± 0.3 °C combined with 1.41 ± 0.11 mg L^{-1} DO caused 100% cumulative mortality within three days of a 96 h experiment. The mortality hazard was greatly elevated relative to normoxic controls at identical or cooler temperatures. Median algal clearance across 25 °C normoxia, 29 °C normoxia, 25 °C hypoxia, and 29 °C hypoxia was 1.26, 0.89, 0.14, and 0.01 L g^{-1} h^{-1}, respectively [5, 6]. These matched comparisons demonstrate rapid compound risk without requiring a synergy label.

A two-factor experiment with Manila clams used 24, 28, and 32 °C and DO concentrations of 1, 2, 4, and 6 mg L^{-1}. Temperature, DO, and their interaction affected survival, behaviour, oxygen consumption, ammonia excretion, and energy-use indicators. Median lethal time under severe combinations ranged from 107 to 228 h, whereas clams survived across the tested DO range at 24 °C [7]. Fixed levels isolate response thresholds, but natural events also include gradual warming, nocturnal cycling, changing food supply, and recovery.

Short-term adjustment can also appear without rapid mortality. During an eight-day dock-side experiment that matched field conditions, eastern oysters encountered water near 27 °C and repeated hypoxia below 2 mg O_2 L^{-1}. Oysters maintained oxygen consumption while valve-opening amplitude fell by approximately 3–4% during hypoxic phases. Soft-shell clams showed heat-related

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metabolic depression and increased oxygen consumption during repeated hypoxia [8]. The contrasting responses show that the same trajectory can impose different costs. Maintained oxygen consumption also does not prove that feeding or growth remained unchanged.

3.2. Oxidative and immune responses

Oxidative and immune responses help explain why a bivalve may remain alive while losing performance. When oxygen supply fluctuates, mitochondrial disturbance and reoxygenation can increase reactive oxygen species. Antioxidant enzymes and stress proteins may rise as compensation, but increased activity is not inherently protective and can consume energy needed for growth or repair. In Manila clams, antioxidant responses at 32 °C and DO at or below 2 mg L^{-1} increased initially and declined as exposure continued [7]. This pattern is consistent with a shift from compensation toward impaired capacity, although it cannot establish a production loss.

Hard-clam gill transcriptomes differed among heat, hypoxia, and combined treatments. Protein processing in the endoplasmic reticulum and ubiquitin-mediated proteolysis were prominent under combined exposure, while a related analysis documented extensive HSP70 gene expansion and stress-responsive transcription [9, 10]. These findings identify cellular defence pathways and show that combined exposure can reorganize the response profile. They do not quantify feeding, growth, survival, or economic loss. Molecular signals alone cannot establish effects on farm output without corresponding organismal and production endpoints.

3.3. Survival, feeding, growth and potential reproductive consequences

The strongest direct evidence concerns survival and short-term performance. The scallop experiment shows an acute collapse in both survival and clearance when warming overlaps with low DO [6]. The Manila-clam results show that the time available for intervention contracts as temperature rises and DO falls [7]. In contrast, the oyster and soft-shell clam experiment shows that some species maintain oxygen consumption or alter metabolism during repeated hypoxia [8]. These outcomes cannot be ranked without considering species, acclimation, feeding regime, and duration.

Growth can be reduced by oxygen cycling that is less severe than an acute lethal treatment. In nine field-linked flow-through experiments, alleviating natural nocturnal hypoxia increased mean juvenile bivalve growth by 20%, with experiment-specific changes from 0 to 70% [5]. The study did not manipulate temperature, so it measures an oxygen-mediated component of summer exposure rather than an MHW effect. Its practical lesson is that repeated hours below a threshold and the opportunity to recover may matter more than a moderate daily mean.

Reproductive consequences remain plausible but are not established by the available matched temperature × DO evidence. If warming raises maintenance demand, hypoxia restricts aerobic ATP production, and valve closure reduces food acquisition, less energy may remain for gametogenesis, spawning, egg provisioning, or larval development. This pathway follows from performance changes and energy allocation, but it is an inference rather than a direct measurement of reproductive output. Future studies should measure gonadal development, spawning, larval production, recruitment, and harvestable biomass in the same exposure sequence.

3.4. Interpreting combined effects

Paired treatments do not yield one response pattern. Hypoxia sharply magnified warming effects on scallop clearance and survival, whereas other bivalves maintained oxygen consumption while

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altering pumping or metabolism [6-8]. Such contrasts may reflect species, exposure profile, and physiological strategy. An additive response can still matter biologically; a non-additive result may be interactive, synergistic, or antagonistic only when the additive expectation and statistical departure are specified. Table 1 separates joint exposure from regional attribution, molecular evidence, and oxygen-only field evidence, so none is mistaken for farm-scale proof.

Table 1. Evidence hierarchy and quantitative results for oxygen limitation associated with marine heatwaves in commercially relevant bivalves [2-3, 5-10]

Study context or taxon	Exposure	Duration	Endpoint	Quantitative or primary result	Evidence class	Interpretive limit
Northern bay scallops	25 vs 29.0 ± 0.3 °C; normoxia vs 1.41 ± 0.11 mg L^{-1} DO	96 h	Survival; algal clearance	100% mortality within 3 d at 29 °C plus hypoxia; median clearance 1.26, 0.89, 0.14, and 0.01 L g^{-1} h^{-1} across treatments	Direct temperature × DO factorial	Acute adult experiment; not a farm-scale production estimate
Manila clams	24, 28, and 32 °C × 1, 2, 4, and 6 mg L^{-1} DO	Lethal-time endpoint	Survival; behaviour; respiration; excretion; enzymes	Temperature × DO effects; median lethal time 107–228 h under severe combinations; survival across DO at 24 °C	Direct temperature × DO factorial	Fixed levels simplify natural onset, cycling, and recovery
Hard clams	Heat, hypoxia, and combined treatments	3 d	Gill transcriptome	Endoplasmic-reticulum protein processing and ubiquitin-mediated proteolysis prominent under combined exposure	Direct combined molecular evidence	No matched feeding, growth, or survival endpoint
Hard clams	Heat and hypoxia exposure series	3 d	HSP70 genes; stress transcription	Large HSP70 family and stress-responsive expression documented under heat and hypoxia	Molecular contextual evidence	Molecular signals are not production outcomes
Eastern oysters and soft-shell clams	Heatwave near 27 °C with repeated DO below 2 mg O_2 L^{-1}	8 d	Oxygen consumption; pumping; valve opening	Oyster oxygen consumption maintained while valve-opening amplitude fell about 3–4%; clam responses differed	Direct combined exposure	Short exposure; physiological responses were species-specific
Baltic coastal seabed	Bottom MHW at least 17 °C for at least 10 d; depth mainly below 20 m	Multidecadal reanalysis	Bottom temperature and oxygen	Oxygen difference reached about −3 mL L^{-1}; solubility explained most of the decline	Regional attribution	No farm or bivalve response measured
Five economically important bivalves	Two +4 or +8 °C events, each 3 d, separated by 3 d recovery	Two event cycles	Survival; metabolic and enzyme traits	Bay scallops and Paphia undulata reached 100% mortality during the first +8 °C event; three species retained up to 90% survival	Heat-only comparative evidence	Shows thermal vulnerability, not oxygen mediation

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Table 1. (continued)

Juvenile hard clams, oysters, and scallops	Natural nocturnal DO cycling with aeration treatment	Nine experiments over three summers	Growth; survival	Aeration increased mean growth 20%, with experiment-specific changes from 0 to 70%; controls averaged 3 h per night below 3 mg L^{-1}	Hypoxia-only field-linked evidence	No heat manipulation; not an MHW estimate

4. Factors modifying environmental coupling and bivalve responses

4.1. Biological factors

Species, life stage, body condition, and acclimation alter metabolic demand and tolerance. A comparative heatwave experiment on five economically important bivalves found 100% mortality in bay scallops and Paphia undulata during the first +8 °C event, while three other species retained up to 90% survival [3]. Because DO was not manipulated, this demonstrates thermal vulnerability, not oxygen mediation. Recurrent heatwaves can also alter Manila-clam metabolic and antioxidant responses depending on intensity [11]. The dock-side experiment showed different strategies in oysters and soft-shell clams [8].

Life stage remains underrepresented in direct compound studies. Larvae and juveniles may differ from adults in energy reserves and recovery capacity, although direct life-stage comparisons under combined warming and hypoxia remain scarce. Thermal history may shift enzyme capacity and behaviour, but acclimation to moderate warming does not demonstrate tolerance to severe low dissolved oxygen. Comparisons should preserve species, stage, prior exposure, and endpoint rather than rank taxa by one temperature metric.

4.2. Site conditions and exposure history

The same thermal anomaly can affect farms differently. A flushed site may recover before energy reserves are exhausted; an enclosed, organic-rich site may not. Nutrient, biodeposition, sediment, and stocking loads alter oxygen demand, while food supply determines whether increased pumping offsets its metabolic cost. These controls can make a modest marine heatwave consequential when dissolved oxygen is already low, whereas strong water exchange can decouple warming from prolonged oxygen loss. Risk assessment should follow local water and animal status, not regional temperature alone (See Table 2).

Exposure timing can matter more than the peak. Repeated nocturnal hypoxia may limit feeding and repair even when daytime oxygen recovers; closely spaced heatwaves may leave little time to rebuild reserves. Farm records should retain minimum DO, time below threshold, warming rate, recurrence, and reoxygenation. Similar daily means can impose vastly different physiological costs.

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Table 2. Biological and site factors modifying heat and oxygen coupling and bivalve responses [2-5, 8, 11]

Modifier	Pathway to exposure or response	Evidence example	Interpretation	Limit for use
Species and life stage	Thermal ceiling, oxygen regulation, reserves, and developmental demand differ	Comparative heatwave trials showed large species contrasts; life-stage differences remain insufficiently tested under direct compound exposure	Thresholds should be evaluated separately across taxa and life stages	Do not rank species across unmatched stressors or life stages
Thermal history and acclimation	Prior exposure shifts metabolic and behavioural capacity	Repeated heat exposure can alter survival, enzyme activity, and the timing of compensation	History changes the cost of a new event	Acclimation to heat does not prove tolerance to low DO
MHW intensity and duration	Controls solubility loss, demand, stratification, and cumulative energy cost	Regional seabed events lasted at least 10 d; severe experimental warming caused mortality in sensitive taxa	Magnitude and time must be analysed together	Regional temperature thresholds are not universal
Background DO	Sets the oxygen reserve before warming begins	Nocturnal field sites ranged from 0.11 to 3.9 mg L^{-1} and 1 to 23 h of hypoxia	A modest MHW may matter when starting DO is already low	A single daytime or mean value can miss risk
Water depth and flushing	Regulates heat retention, ventilation, and recovery	Shallow coastal settings can experience seabed heatwaves and oxygen decline	Exchange determines whether heat and oxygen remain coupled	Depth alone is not a proxy for exchange
Eutrophication and organic loading	Increases algal production and microbial decomposition	Nutrient and organic inputs can create background hypoxia before warming	Background hypoxia may precede and then be amplified by an MHW	Local load and residence time need measurement
Sediment oxygen demand	Consumes oxygen near bottom-planted or caged bivalves	Benthic respiration can draw down oxygen in the animal exposure layer	Sensor placement should represent near-bottom conditions	Farm-specific demand during MHWs is poorly quantified
Stocking density and biodeposition	Raises animal respiration and supplies degradable organic matter	High biomass can modify local demand, but direct MHW attribution remains limited	Density may alter both demand and background oxygen loss	Do not claim a universal density effect without site trials
Food availability	Determines energy acquisition and modifies pumping costs	Maintained oxygen consumption does not guarantee adequate feeding or growth	Food supply can change the balance between compensation and loss	Chlorophyll and seston quality can confound exposure and growth
Recurrence and recovery time	Controls reserve depletion, reoxygenation stress, and repair	Nocturnal cycling and recurrent heatwaves can produce cumulative effects	Hours below threshold and time to recovery belong in warning metrics	Static experiments may miss cumulative and recovery effects

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5. Monitoring and aquaculture management implications

5.1. Integrated baseline monitoring and heat-triggered escalation

Routine DO monitoring should continue whether or not an MHW is forecast. Sensors are most informative near the cultured animals, including near the bottom and during the interval from sunset to pre-dawn, when background and nocturnal hypoxia may otherwise be missed. A temperature anomaly should escalate the baseline programme rather than start it. Sampling intervals can be shortened, depth coverage expanded, and records can distinguish oxygen decline that is induced, amplified, or merely coincident with warming. The risk record should combine temperature anomaly, minimum DO, hours below a local threshold, recurrence, and time to reoxygenation with valve activity, feeding, growth, and mortality. High-frequency records can identify false alarms and missed events. Thresholds should specify species, life stage, temperature, duration, and recovery context.

5.2. Targeted interventions and their evidence limits

Aeration has direct evidence for reducing the oxygen-mediated component of nocturnal exposure. Across nine field-linked experiments, alleviating natural hypoxia increased mean bivalve growth by 20%, with gains from 0 to 70%; average improvement was 23% for scallops and 30% for oysters [5]. Aeration can raise oxygen around animals when hydrodynamics allow, but it cannot remove direct thermal injury. Its value depends on mixing depth, biomass, food supply, and capacity.

A temperature and DO warning can guide routine decisions. During a high-risk window, operators may postpone handling, reduce organic loading, improve exchange, mix selected units, reduce stocking in hotspots, or harvest early when condition and logistics allow. These are options, not universal prescriptions. Site trials should record cost, changes in temperature and DO, animal response and unintended consequences.

5.3. Climate-resilient production systems

Longer-term resilience begins with site and production design. Heatwave history, nocturnal hypoxia, depth, flushing, sediment condition, nutrients, and food supply can inform species choice, stocking, and the production calendar. Comparative studies show large species differences, while broader planning links monitoring with operational readiness and social capacity [3, 4, 11]. Breeding, cohort diversification, revised calendars, and exchange infrastructure may reduce exposure, but benefits should be tested under combined dynamic conditions. The endpoint is reliable harvestable biomass under site-specific stress histories.

6. Limitations and future research priorities

6.1. Limits of the current evidence

Few studies connect environmental exposure with animal response, farm production, and economic loss within a single experimental framework. Regional environmental assessments attribute oxygen change without measuring bivalve physiological status, whereas laboratory factorial studies isolate temperature and dissolved oxygen but simplify natural hydrodynamics. Field-linked trials connect nocturnal oxygen to growth without manipulating temperature; comparative heatwave studies provide thermal context rather than evidence of oxygen mediation. Definitions of extreme thermal

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events vary. Warming trajectories are not static high temperatures, and dissolved oxygen thresholds shift with taxon, developmental stage, acclimation, and exposure duration. Molecular responses cannot substitute for production or economic data. Farm-specific biodeposition dynamics during heatwave-associated oxygen limitation remain poorly quantified.

6.2. Priorities for attribution, experiments and farm-scale validation

Field work should classify induced, amplified, and co-occurring events using oxygen budgets and high-frequency records. Near-bottom and overnight measurements are essential to separate thermal, oxygen-mediated, and background environmental effects. Experiments should pair factorial controls with gradual warming, nocturnal low dissolved oxygen, repeated hypoxia and reoxygenation cycles, recovery periods, and farm-derived exposure sequences. Common endpoints measured across life stages should link physiology to feeding, growth, mortality, harvestable biomass, and economic outcome. Site-level validation is necessary before risk frameworks can be applied in practical aquaculture management.

7. Conclusion

Marine heatwaves should not be treated as simply parallel to hypoxia in coastal bivalve aquaculture. Warming can lower oxygen availability through reduced solubility, stratification, restricted ventilation, and increased biological consumption, while the animals themselves may need more oxygen to maintain metabolism. The resulting imbalance can be initiated by an MHW, intensified when warming meets pre-existing hypoxia, or observed as a co-occurrence without proven causation. Background oxygen loss also develops independently from nutrients, organic loading, benthic and nocturnal respiration, restricted exchange, and farm biodeposition.

The paired experiments point to a conditional response rather than a universal rule. Some combinations rapidly reduced feeding and survival; other bivalves maintained oxygen consumption while changing pumping or metabolic strategy. Species, stage, thermal history, exposure duration, and recovery help explain these differences. Additive effects can still be serious, and a statistically significant temperature × DO interaction is not automatically synergistic. Nocturnal minima and time below a threshold may matter even when daily mean DO looks moderate. Short-term physiological or molecular signals still have not been fully linked to reproduction, harvestable biomass, or economic loss.

For farms, the practical question is not which single temperature or DO value applies everywhere. It is whether local exposure has moved from short-term compensation toward sustained performance loss. Near-bottom and overnight temperature and DO records should provide the baseline; anomalous warming should trigger denser sampling and broader depth coverage. Aeration can reduce the oxygen-mediated component when it reaches the culture layer, but direct thermal injury remains. Decisions about exchange, organic loading, density, handling, and harvest should be tested against site conditions and operating cost.

The remaining gaps are clear. Direct temperature × DO studies are few, reproductive evidence is scarce, laboratory exposures are often static or short, and long-term farm-scale economic data are rare. Future work should pair dynamic experiments with high-frequency field attribution, common endpoints across life stages, and farm validation. Linking physiological responses to growth, harvestable biomass, and economic outcome will show when a biomarker is compensatory and when an intervention changes a decision-relevant result.

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