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Effects of Temperature Variations on Growth and Survival of Abalone

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Abstract Temperature variation is a critical environmental factor influencing the physiological performance, growth, and survival of abalone in aquaculture systems. This study systematically reviews and analyzes the effects of temperature fluctuations on abalone culture by integrating biological characteristics, environmental temperature dynamics, growth performance responses, survival outcomes, and underlying metabolic mechanisms. Results indicate that abalone exhibits a relatively narrow optimal temperature range, within which growth rate, feeding efficiency, and energy allocation are maximized. Deviations from this optimal range, particularly under elevated temperature conditions, significantly reduce growth performance and increase mortality risk due to intensified metabolic demand, oxygen limitation, and physiological stress. Low-temperature stress similarly suppresses metabolic activity and feeding behavior, leading to reduced growth and delayed development. At the molecular level, temperature fluctuations influence enzyme activity, respiratory metabolism, and gene expression associated with stress response pathways. Seasonal and climate-driven temperature variability further exacerbates these effects in intensive aquaculture systems. A case study of commercial abalone farms demonstrates that extreme temperature events can cause substantial production losses, while effective temperature regulation strategies such as water cooling, depth adjustment, and environmental monitoring can mitigate adverse impacts. Overall, this study highlights the importance of precise temperature management for maintaining abalone health, improving production efficiency, and ensuring the sustainability of aquaculture operations.

Keywords Abalone; Temperature variation; Growth performance; Survival rate; Aquaculture management

1 Introduction

Global warming and more frequent marine heatwaves are intensifying temperature variability in coastal waters, directly challenging aquaculture species such as abalone. Abalone farms, which typically rely on ambient coastal water with limited control over temperature and other variables, already experience mass summer mortalities and reduced growth when thermal conditions exceed species' tolerance ranges (Morash and Alter, 2016). As a result, temperature sensitivity has emerged as one of the key bottlenecks for the sustainable expansion and economic stability of the abalone farming industry worldwide (Liu et al., 2022). Abalone are poikilothermic marine invertebrates whose physiological performance, including growth, reproduction and survival, is tightly constrained by water temperature regimes. Elevated temperatures can compromise multiple life stages, suppressing larval development, stunting growth and increasing susceptibility to disease, with documented mass mortalities during anomalously warm summers and marine heatwaves (Barkan et al., 2025). In abalone culture regions such as southern China, seasonal peaks approaching 30 °C now regularly drive severe summer mortality events, highlighting a narrowing safety margin between optimal and lethal conditions for farmed stocks. From a broader physiological perspective, temperature fluctuations alter core processes in marine invertebrates, including metabolism, cardio-respiratory function, mitochondrial performance and cellular protective mechanisms (Whiteley and Mackenzie, 2016; Kazmi et al., 2022).

In abalone specifically, both rapid and chronic thermal stress can drive increased metabolic rates, oxidative stress, altered enzyme activities, and changes in gene expression that influence growth efficiency and survival probabilities (Kang et al., 2019). Yet, some exposure regimes, such as naturally fluctuating temperatures, may allow physiological adjustment that buffers animals against lethal extremes (Xu et al., 2020). Despite growing recognition of temperature as a critical constraint for abalone aquaculture, key questions remain regarding how specific patterns

of temperature variation-such as chronic warming, short heatwaves, or diel fluctuations-affect growth trajectories and survival across life stages and genotypes.

The present study therefore aims to quantify how realistic temperature variation regimes influence growth and survival of farmed abalone, and to relate observed performance to putative stress thresholds identified in previous physiological and omics studies (Chen et al., 2016). It is hypothesized that moderate fluctuations around sub-lethal means will support better growth and survival than sustained exposure near upper tolerance limits, and that these responses will provide practical guidance for temperature management, selective breeding, and site selection in abalone farming under climate change (Xu et al., 2020).

2 Biological and Ecological Characteristics of Abalone Related to Temperature Response

2.1 Physiological characteristics and growth/development patterns of abalone

Abalone are poikilothermic, so temperature strongly shapes growth trajectories and optimal size-at-age in culture and the wild. In integrated abalone-kelp systems, specific growth rate of *Haliotis discus hannai* shows a clear quadratic relationship with temperature in each size class, and optimal culture temperatures differ for small (<15 g) versus larger (>15 g) individuals, indicating size-dependent thermal optima for growth (Fang et al., 2018). Experimental work on Australian hybrid abalone similarly shows that growth, weight gain and shell extension all increase from 12 °C to 22 °C, confirming that warmer conditions within the tolerable range enhance growth performance during the grow-out phase (Hassan et al., 2023). Temperature effects on development also act indirectly through food quality and nutrition. For juvenile red abalone, growth and condition are significantly better when fed dulse cultured at higher temperatures, because warmer-grown seaweed has higher protein and nitrogen content, linking primary producer thermal responses to abalone growth potential (Rizzo et al., 2024). At larger spatial scales, physiological thermal optima for scope for growth around 24 °C, with an upper limit near 30 °C, help explain observed distribution patterns of wild abalone along thermal gradients (Lluch-Cota et al., 2023).

2.2 Respiratory metabolism and energy allocation mechanisms

Temperature directly modulates respiratory metabolism in abalone, altering oxygen consumption, excretion and substrate use. In *Haliotis discus hannai* exposed to semidiurnal temperature fluctuations between 20 °C-26 °C, metabolic rate tracks short-term temperature changes and rises sharply under stable warm conditions, while similar ammonia excretion across treatments indicates that elevated energy demands are partly met by protein catabolism (Kang et al., 2019). Similarly, cold-acclimated *Haliotis midae* show increased oxygen consumption and nitrogen excretion during acute warming, reflecting greater reliance on proteins as metabolic fuel under short-term thermal stress. With longer-term thermal exposure, abalone can adjust energy allocation among metabolic pathways. After a month at elevated temperatures, *H. midae* partially compensate by reducing mass-specific oxygen and nitrogen fluxes and shifting towards carbohydrate use at 22 °C, indicating acclimatory changes in fuel selection. Metabolomic and transcriptomic studies in juvenile and hybrid abalones under heat stress show coordinated activation of aerobic pathways (TCA cycle, oxidative phosphorylation) alongside anaerobic glycolysis, supporting ATP production when oxygen demand rises and solubility drops at high temperatures (Xu et al., 2020).

2.3 Thermal tolerance ranges and ecological distribution characteristics

Thermal tolerance in abalone is often quantified using critical temperatures or cardiac performance thresholds, revealing interspecific and hybrid differences. In *Haliotis discus hannai*, *H. gigantea* and their hybrid, Arrhenius break temperatures of cardiac performance, as well as lethal limits and critical thermal maxima, are highest in the hybrid (≈32.5 °C), intermediate in *H. gigantea*, and lowest in *H. discus hannai*, indicating enhanced tolerance and suggesting that warming will differentially impact these taxa in culture (Chen et al., 2016). Size-dependent analyses in Australian hybrid abalone show that, under slower, ecologically realistic warming, larger individuals have lower critical thermal maxima, implying that marine heatwaves and chronic warming may preferentially favour smaller, less fecund animals in farms and wild populations (Holland et al., 2023). At population and species scales, acclimation history and oxygen availability further modulate realized thermal niches and distribution. Work integrating scope for growth with sea-surface temperature shows that wild abalone densities off Baja California are

constrained by a trade-off between mean temperatures near physiological optima (~24 °C) and the risk of frequent excursions into suboptimal or lethal warmth in highly variable environments, emphasizing the importance of temporal variability as a concurrent limiting factor (Lluch-Cota et al., 2023). A mechanistic "metabolic index" calibrated for red abalone shows that warming and deoxygenation shift the temperature of maximal oxygen supply to cooler values, shrinking viable habitat-especially for larger individuals-and offering a framework to link physiology with projected range contractions under climate change (Duncan et al., 2023).

3 Temperature Variability in Marine Aquaculture Environments

3.1 Seasonal and diurnal temperature variation patterns in natural marine waters

In shallow coastal habitats typical of many aquaculture sites, temperature is dominated by a strong seasonal cycle, with warm summers and cold winters, overlaid by rapid short-term variability. Hourly records from a 5 m coastal site in the eastern Adriatic show that seasonal changes are prevalent, but diurnal changes are quasi-persistent year-round, and rapid shifts during stratified seasons can reach 2 °C per hour, with marine heatwaves and cold spells strongest in spring and summer (Vilibić et al., 2022). Similar patterns emerge in the northern Yellow Sea, where bottom temperatures at aquaculture sites exceed 20 °C in late summer and fall below 5 °C in winter, with some locations experiencing fortnightly oscillations of several degrees linked to tidal currents and thermal fronts. Such high-frequency variability has direct implications for benthic invertebrates and farmed stocks. The Adriatic study notes that rapid changes of up to 2 °C per hour may affect benthic communities and species physiology, particularly under global warming where environmental conditions are already near tolerance thresholds. In the Yellow Sea, modelled bottom-temperature variability has been linked to damage in bottom-cultured scallops, and a spatial index of variability has been proposed to guide site selection and design of temperature-stress experiments, a concept directly transferable to abalone aquaculture planning (Asplin et al., 2021).

3.2 Occurrence patterns of extreme high- and low-temperature events

Beyond regular cycles, extreme warm events—marine heatwaves—are increasingly recognized as a major threat to marine ecosystems, fisheries and aquaculture. A hierarchical framework defines marine heatwaves as prolonged, discrete, anomalously warm water events with temperatures above the 90th percentile for at least five days, emphasizing metrics such as duration, intensity and spatial extent to enable consistent comparison of events and their biological impacts (Hobday et al., 2016). Global analyses show that the most extreme marine heatwaves preferentially occur in summer, when mixed layers are shallow and winds weak, and that their duration has increased multi-decadally, with about 60% of the ocean experiencing its longest-duration event since 2010. Historical reconstructions over 1925-2016 reveal that globally, marine heatwave frequency and duration increased by 34% and 17%, respectively, leading to a 54% rise in annual marine heatwave days, largely attributable to rising mean ocean temperatures (Oliver et al., 2018). For aquaculture, regional case studies in the western Mediterranean show marine heatwaves have become about three times more frequent with 50% longer durations compared with the 1980s, including a 2022 event where anomalies up to 4.2 °C persisted the entire summer—conditions that exceeded fish thermal welfare thresholds and raise concerns for farmed stocks (Atalah et al., 2024).

3.3 Long-term trends in seawater temperature under climate change

Long-term observational and modelling studies show that coastal and open-ocean temperatures are rising, reshaping the background conditions on which shorter-term variability is superimposed. A global coastal analysis using CMIP6 models projects significant coastal sea surface warming, with most basins experiencing about a 1 °C increase by mid-century and some regions exceeding 2 °C anomalies relative to 1995-2014, indicating that nearshore systems where aquaculture is concentrated will face faster and more variable warming than previously observed (Varela et al., 2023). High-resolution analyses of coastal sea surface temperatures over three decades similarly report that 71% of the world's coastlines are significantly warming, with heterogeneous rates, a marked decrease in extremely cold events on 46% of coasts, and more frequent extremely hot days on 38%, as well as earlier onset of the warm season in many temperate regions. At the global scale, ocean heat content has increased markedly, with reanalysis indicating a 62-year warming signal and a statistically significant acceleration in recent decades, meaning that a growing fraction of the ocean now reaches its maximum yearly heat content in the most recent years (Storto and Yang, 2024).

Climate-model projections focused on northern large marine ecosystems further suggest that most future sea surface temperature change will arise from a positive shift in the mean, with only modest changes in variability, leading to a substantial increase in warm extremes and decrease in cold extremes; by late century, many regions are projected to be warmer every year than the warmest year of the late twentieth century (Alexander et al., 2018).

4 Effects of Temperature on Growth Performance of Abalone

4.1 Responses in growth rate and body weight gain

Growth performance in abalone shows a pronounced, often non-linear dependence on temperature. For *Haliotis midae* fed formulated diets, growth rate and feed consumption increase between 12 °C-20 °C, but both decline sharply from 20 °C-24 °C, with deterioration in protein efficiency ratio and feed conversion, indicating that temperatures above the natural range rapidly constrain weight gain (Morash and Alter, 2016). Size-dependent optima are also evident: juvenile *Haliotis iris* grow fastest at ~22 °C, whereas larger individuals peak at 17 °C-18 °C, suggesting that ideal grow-out temperatures decline as abalone increase in size (Steinarsson and Imsland, 2003; Searle et al., 2006). Integrated multitrophic aquaculture studies confirm that both size and temperature significantly shape specific growth rate (SGR) in *Haliotis discus hannai*. SGR follows a quadratic relationship with temperature within each size class, with small abalone (<15 g) performing best at 20 °C-22 °C and larger individuals at 15 °C-20 °C, underlining the need to tailor temperature regimes to body size for maximal body-weight gain (Fang et al., 2018). Long-term acclimation can also modify growth responses: domesticated *H. discus hannai* populations from warmer regions show enhanced thermal tolerance and improved capacity to redistribute energy under high temperatures, supporting better growth under warming conditions than naive northern stocks (Yu et al., 2023).

4.2 Changes in feeding behavior and digestive efficiency

Feeding behaviour and ration size are strongly temperature dependent. In *H. midae*, daily food intake rises from about 8.1% of wet flesh mass at 14 °C to 11.4% at 19 °C, indicating higher consumption at warmer temperatures, while a clear nocturnal feeding rhythm (16:00-08:00) supports nighttime grazing as temperatures and activity peak. In green abalone *Haliotis* fulgens, feed consumption increases at night and is higher at 25 °C than at 20 °C across photoperiods, yet growth and survival decline at 25 °C, suggesting that elevated intake cannot fully offset thermal stress and reduced conversion efficiency. Temperature also influences digestive efficiency and enzyme activity. Moderate heat stress (5 °C above ambient for six weeks) elevates metabolic rates in *Haliotis* rufescens and *H. iris*, but apparent digestibility of organic matter, protein and carbohydrate remains unchanged, indicating that digestive efficiency can be maintained despite higher energetic demand (Frederick et al., 2022). In post-weaned greenlip abalone, raising temperature from 14 °C to 20 °C significantly increases trypsin, amylase and lipase activities, and improves feed conversion at 20 °C, suggesting that warmer conditions within the optimal range enhance enzymatic capacity and nutrient utilization (Bansemer et al., 2023).

4.3 Impacts on shell formation and energy allocation

Temperature affects shell formation both through calcification rates and through molecular pathways of biomineralization. In *Haliotis* tuberculata, calcification rates are lower in cool seasons and higher in warmer seasons, paralleling temperature-driven changes in respiration and excretion and indicating increased shell deposition when thermal and metabolic conditions are favourable (Chapperon et al., 2018). Under combined warming and acidification, however, reconstructed shells of *H. discus hannai* develop corroded and irregular aragonite plate microstructures, and key nacre protein genes (Hdh-AP7, Hdh-AP24) that induce crystal formation become highly sensitive to thermal stress, demonstrating direct damage to shell quality through disturbed expression of biomineralization genes. (Zheng et al., 2020). Energy allocation under thermal variation reflects a balance between maintenance, growth and shell production. In *H. discus hannai* cultured in an abalone-kelp IMTA system, all measures of carbon allocation (including respiration, excretion and growth carbon) increase with temperature, and optimum regimes are size-specific, implying that higher temperatures drive greater overall energy throughput but require careful matching of food supply to sustain shell and tissue growth (Fang et al., 2018). Physiological studies under fluctuating and high summer temperatures show that elevated metabolic and ammonia excretion rates at warm conditions can deplete tissue energy reserves when food intake does not keep pace, leading to disturbed maintenance and reduced growth, which likely includes compromised shell deposition (Kang et al., 2019).

5 Effects of Temperature on Survival and Physiological Stress

5.1 Patterns of survival rate and mortality risk

Elevated temperatures sharply increase mortality risk in abalone, especially when they approach or exceed upper tolerance limits. Continuous exposure of *Haliotis discus hannai* to temperatures above 26 °C reduced survival, increased falling rates, and produced abnormal foot structures, indicating impaired attachment and higher risk of mortality under chronic heat stress (Gao et al., 2024). Field-relevant thermal pollution from nuclear power plant discharge demonstrates that even a 2 °C rise above already warm ambient conditions can cause partial mortality and reduced adhesion in hybrid abalone, underscoring the narrow margin between stressful and lethal temperatures in summer (Barkan et al., 2025). Cold stress also elevates mortality risk and narrows the safe operating window for culture. In *Pacific abalone* exposed for 7 days, survival remained near 100% at 8 °C-10 °C but dropped to 25%-55% at 4 °C across salinities, accompanied by strong oxidative and cellular stress signals in hemolymph. Acclimation history modifies acute survival outcomes; juveniles pre-acclimated at 30 °C for 62 days showed higher survival than 10 °C-acclimated counterparts during a 31 °C heat challenge, highlighting the role of prior temperature exposure in shaping mortality risk under extreme events (Xu et al., 2020).

5.2 Mechanisms of heat stress and oxidative stress responses

At the cellular level, heat stress in abalone disrupts mitochondrial function and elevates oxidative load. Metabolomic analysis of *Haliotis discus hannai* juveniles showed that acute exposure to 31 °C after acclimation led to mitochondrial failure, incomplete oxidative metabolism of amino acids and fatty acids, and accumulation of unstable intermediates, particularly in cold-acclimated animals. In disk abalone, both elevated (25 °C) and depressed (15 °C) temperatures, especially when combined with low pH, increased H_2O_2, malondialdehyde, and antioxidant enzyme activities, demonstrating that departures from optimal temperature trigger oxidative stress and lipid peroxidation (Kim et al., 2023). Protective responses to heat stress are mediated by antioxidant systems and heat shock proteins (HSPs). Reviews and experimental work describe how failure to match increased metabolic demand at higher temperatures leads to excess reactive oxygen species, which are countered by antioxidases and antioxidants as a first defense, followed by induction of HSPs to refold or remove damaged proteins (Xu et al., 2020). Differential expression studies in *Pacific abalone* identify large HSP gene families, with many members up-regulated under heat and cold stress; HSPs in hemocytes in particular are highlighted as reliable markers of thermal condition (Kyeong et al., 2019).

5.3 Changes in immune function and stress resilience

Thermal stress reshapes abalone immune function, often in ways that increase susceptibility to pathogens. In farmed hybrid Greenlip × Blacklip abalone acutely heated from 16 °C to 26 °C and held for a week, antibacterial activity, phenoloxidase activity and neutral red retention times declined significantly and did not recover, while total haemocyte counts rose initially, indicating immunosuppression and persistent cellular stress. Chronic exposure of *Haliotis discus hannai* to sub-optimal temperatures (8 °C, 14 °C, 26 °C) for 30 days altered core immune metrics: low temperature increased haemocyte counts and reactive oxygen species, while both low and high temperatures reduced phagocytic capacity and modulated expression of protease inhibitor genes, especially when combined with bacterial challenge. Temperature also mediates resilience by shaping host-pathogen interactions at the molecular level and biasing immune resource allocation. In *Pacific abalone* hemocytes co-cultured with *Vibrio harveyi*, exposure at 25 °C (vs. 20 °C) caused stronger pro-inflammatory and apoptotic transcriptional responses, with up-regulation of caspase-3 and caspase-7, alongside higher expression of multiple virulence genes in the bacteria, demonstrating that warming simultaneously stresses host cells and enhances pathogen aggressiveness (Lee et al., 2023). Field and laboratory work on *Haliotis* rubra similarly shows that while some immune parameters (e.g., antiviral activity) increase with elevated temperature, prolonged warming depresses antibacterial activity and reveals a negative correlation between antiviral and antibacterial responses, suggesting trade-offs that may leave abalone more vulnerable to bacterial disease under future warming scenarios.

6 Temperature-Driven Metabolic and Molecular Mechanisms

6.1 Changes in respiratory metabolic rate and energy expenditure

Temperature strongly modulates respiratory metabolism and whole-animal energy expenditure in abalone. In *Haliotis discus hannai* exposed to semidiurnal fluctuations (20 °C-26 °C), metabolic rates increased sharply at stable warm summer temperatures and fluctuated in parallel with short-term temperature changes, while ammonia excretion remained similar between fluctuating and stable conditions, indicating high maintenance costs and reliance on protein catabolism to fuel elevated demand (Kang et al., 2019). Under moderate heat stress (5 °C above ambient for six weeks), red abalone (*H. rufescens*) and pāua (*H. iris*) also showed 32% and 57% higher metabolic rates, respectively, confirming that acute warming elevates maintenance metabolism across species (Frederick et al., 2022). Interactions with oxygen availability further constrain thermal windows. In juvenile green abalone (*H. fulgens*), warming under hypoxia and hypercapnia caused respiration rates to fall below values expected from an exponential increase and triggered anaerobic metabolism, indicating a downward shift of the upper critical temperature and a narrowed thermal window (Tripp-Valdez et al., 2017; Tripp-Valdez et al., 2018). Seasonal studies on *Haliotis* tuberculata likewise show lower respiration and calcification in cool seasons and higher rates in warm seasons, emphasizing temperature as a primary driver of temporal variability in energy expenditure (Figure 1) (Chapperon et al., 2018).

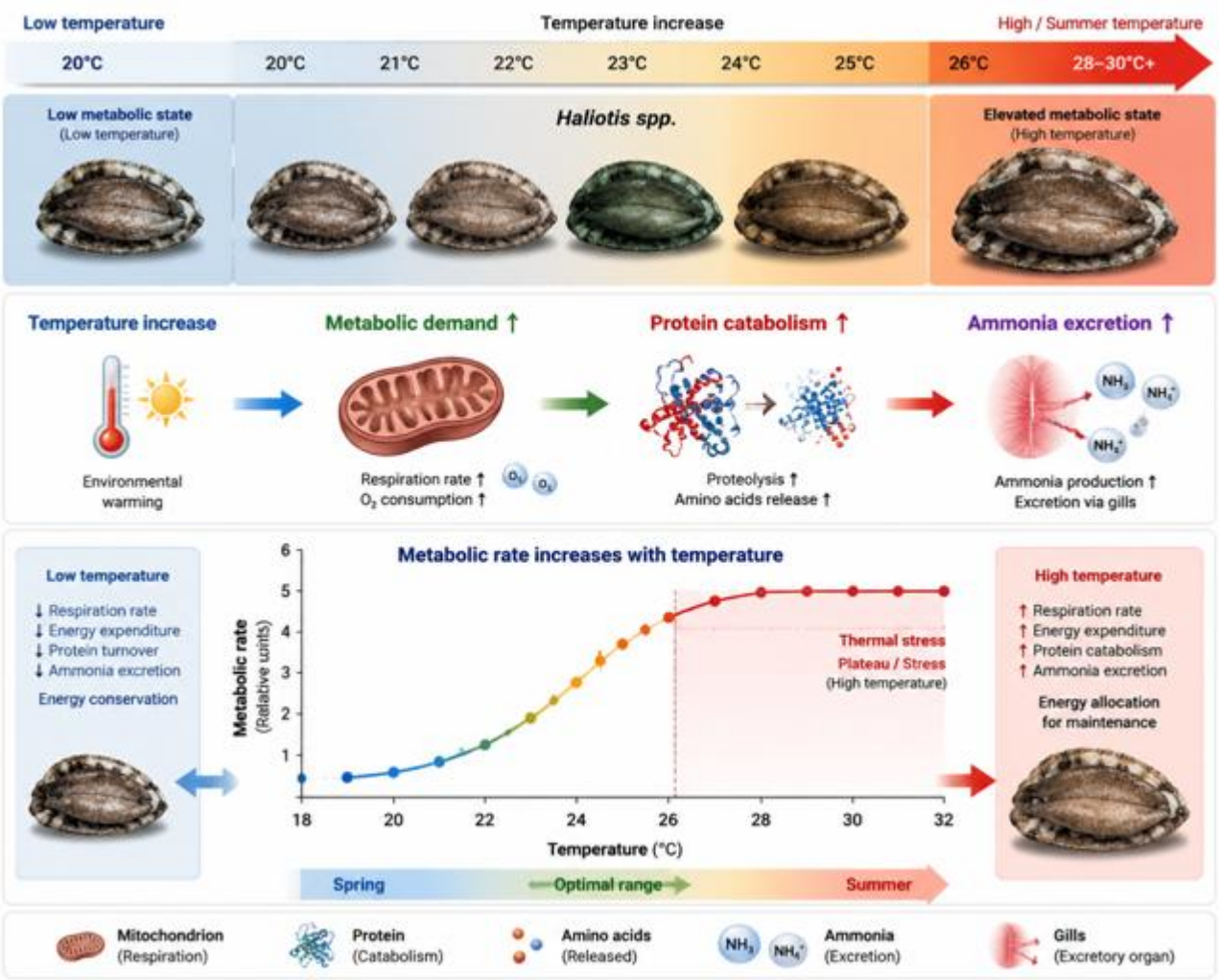

Figure 1 Temperature-driven metabolic regulation in *Haliotis* spp.

6.2 Enzyme activity and metabolic pathway regulation mechanisms

Thermal fluctuations reshape metabolic enzyme activity and pathway use. In *H. discus hannai* exposed to fluctuating temperatures, key metabolic enzymes (PDH, DLD, HIBADH, GDH) were downregulated despite high

overall metabolic rates, while structure-related proteins were upregulated; this pattern indicates altered enzyme activity that reduces protein catabolism and redirects resources to growth under variable regimes. (Kang et al., 2019) Moderate heat stress in *H. rufescens* and *H. iris* also altered digestive enzyme profiles: in red abalone, maltase and aminopeptidases increased at high temperature, whereas in pāua, amylase and β-glucosidase decreased, but overall digestibility remained unchanged, indicating species-specific enzymatic adjustments that maintain nutrient acquisition under elevated demand (Frederick et al., 2022). Metabolomic studies reveal coordinated pathway shifts supporting thermal tolerance. In juvenile *H. discus hannai* acclimated at 10 °C versus 30 °C, acute exposure to 31 °C caused mitochondrial failure and accumulation of unstable intermediates, particularly in cold-acclimated animals, whereas warm-acclimated juveniles showed stronger capacity to produce beneficial metabolites, indicating enhanced regulation of mitochondrial amino-acid and fatty-acid oxidation (Xu et al., 2020). Under low-temperature stress, metabolomics of *H. discus hannai* show that differential metabolites are dominated by carbohydrates and that pathways such as carbohydrate digestion, starch/sucrose metabolism, TCA cycle and pyruvate metabolism are affected, suggesting that regulating carbohydrate use is central to energy supply and antifreeze protection in the cold (Li et al., 2024).

6.3 Gene expression and heat stress response mechanisms

At the molecular level, temperature stress elicits pronounced transcriptomic changes, particularly in genes linked to protein quality control and cellular protection. A meta-analysis of nine RNA-seq datasets across seven *Haliotis* species identified a core set of 74 heat-responsive genes enriched for heat shock proteins, ubiquitin-proteasome components, protein folding, and alternative splicing, indicating a conserved network that manages misfolded proteins and maintains proteostasis under heat stress (Barkan et al., 2025). Acute thermal exposure in *Pacific abalone* induces thousands of differentially expressed genes enriched in protein folding and endoplasmic-reticulum processing; numerous molecular chaperones are strongly upregulated, and ER-associated degradation pathways are activated, suggesting that maintaining ER homeostasis is central to surviving heat stress (Wu et al., 2023). Classical heat shock proteins show acclimation-dependent and rapid inducible responses. In *H. discus hannai*, long-term acclimation at 30 °C or 8 °C leads to elevated basal Hsp70 mRNA levels compared with 12 °C-20 °C, and the temperature that maximally induces Hsp70 during 30-min exposures is higher in warm-acclimated than cold-acclimated gills, demonstrating plastic shifts in induction thresholds. In *H. discus hannai* exposed to 26 °C-28 °C, survival declined and adhesion and foot structure were impaired, accompanied by increased antioxidant enzyme activities and significant upregulation of Hsp90, highlighting cascades from organismal performance to cellular defense as temperatures exceed 24 °C-26 °C.

7 Case Study: Impact of Seasonal Temperature Fluctuations in Intensive Abalone Farming Systems

7.1 Analysis of temperature variations and production performance in typical farming areas

Intensive abalone farming systems commonly experience pronounced seasonal and short-term thermal variability that shapes growth and production efficiency. In Australia, culture temperatures for hybrid abalone typically fluctuate between about 10 °C in winter and 25 °C in summer, far outside the reported thermal optima of ~17 °C-18 °C for parental species, and high summer mortality is recognized as a major constraint to economic performance (Hassan et al., 2023). Land-based systems with well-controlled temperature demonstrate that maintaining water in a stable, warm but sub-optimal range markedly improves predicted growth, confirming that temperature adjustment is a dominant driver of production performance in indoor cultures (Khiem et al., 2023). Field investigations in sea-based farms highlight how seasonal warming can progressively erode physiological condition. In Fujian, southern China, two-year-old *Pacific abalone* reared from April to October experienced a cumulative mortality of 58.58%, with seawater temperature showing a significant positive correlation with mortality and progressive depletion of protein, glycogen and non-esterified fatty acids toward late summer (Lin et al., 2017). At the same time, antioxidant indices (SOD, total antioxidative capacity) first increased and then declined in September and October, indicating that compensatory defense responses were eventually overwhelmed, with likely consequences for growth and harvest yields (Lin et al., 2017).

7.2 Actual impacts of high/low-temperature events on growth and survival

Short-term high-temperature events superimposed on seasonal warming can trigger sharp increases in mortality and physiological stress. In suspended-cage culture adjacent to a tidal-mixing front, *Pacific abalone* exposed to stable high summer temperatures showed elevated metabolic rates and experienced summer mortality, whereas cages experiencing semidiurnal fluctuations between 20 °C-26 °C had no summer mortality, suggesting that intermittent low-temperature periods can buffer lethal impacts. (Kang et al., 2019) In controlled trials with greenlip abalone, survival remained >95% at 18 °C-22 °C but fell by up to 50% at 26 °C when animals were fed a commercial diet, revealing that modest additional warming above 22 °C can halve survival in larger, market-sized stock over several weeks.

Epidemiological analysis of commercial farms confirms that summer mortality risk is tightly linked to thermal extremes. A case-control study of greenlip and hybrid abalone in Australia showed that the risk of summer mortality doubled for every 2 °C increase in maximum weekly water temperature, with interactions involving age, previous mortality history, feed rate and post-grading mortality further modulating outcomes (Figure 2) (Bansemer et al., 2023). Continuous laboratory exposures of *Haliotis discus hannai* to temperatures above 26 °C likewise reduced survival, increased falling rates and caused abnormal foot structures, indicating compromised attachment and heightened mortality risk when summer peaks exceed species-specific thresholds.

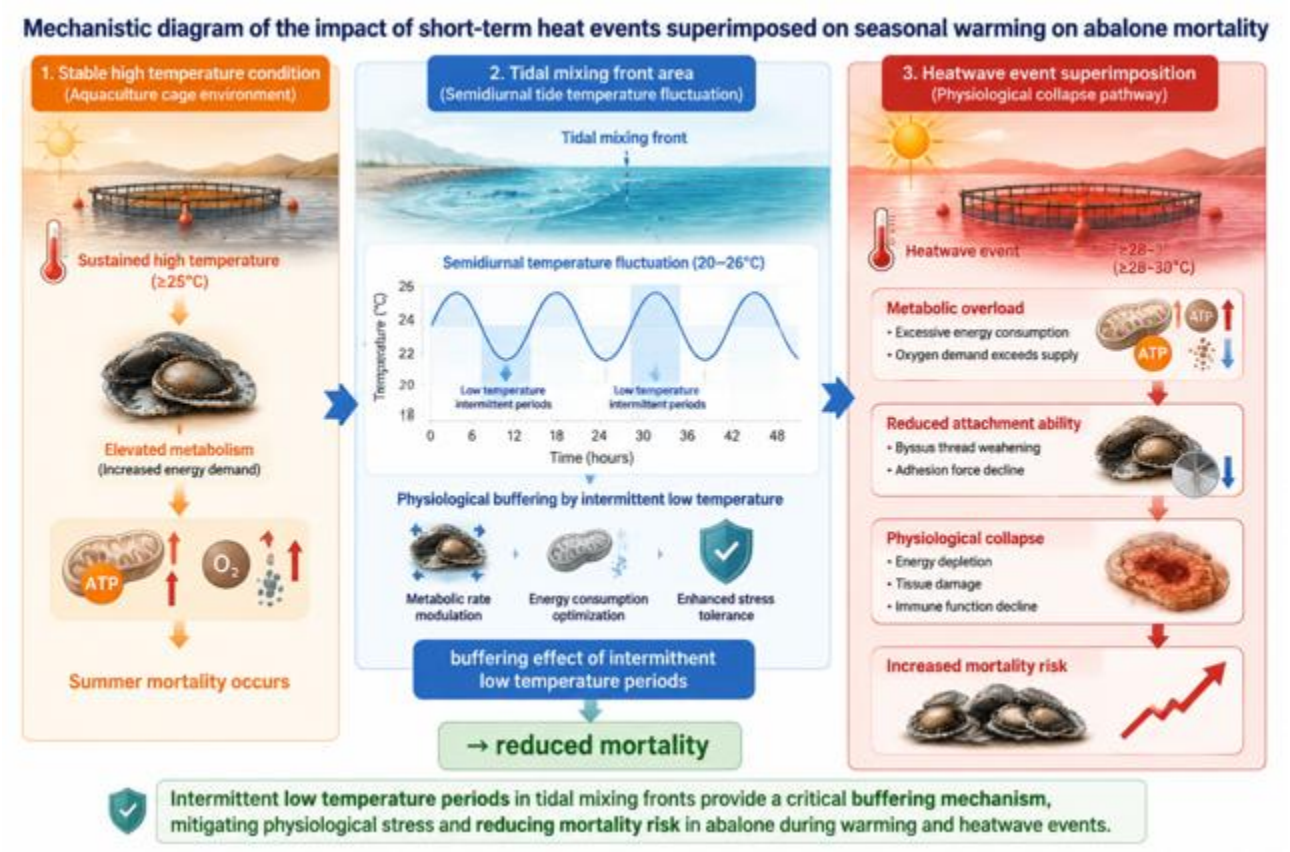

Figure 2 Buffering effects of short-term temperature fluctuations on summer mortality in *Haliotis* spp.

7.3 Evaluation of temperature control measures and farming profitability

Because open coastal farms often cannot economically control temperature, management has focused on nutritional and system-design strategies to mitigate seasonal stress. In hybrid abalone reared at 12, 17 and 22 °C, higher dietary protein (up to 410 g /kg) improved weight gain, specific growth rate and feed conversion, particularly at 22 °C, and did so without compromising flesh quality, indicating that diet optimization at higher temperatures can shorten culture duration and “profit maximisation” despite seasonal warming (Hassan et al., 2023). Similarly, summer-mortality experiments show that providing live macroalgae (Ulva lactuca) at 26 °C maintained survival above 97%,

whereas a standard commercial diet resulted in 35%-50% mortality, demonstrating that targeted dietary interventions can substantially reduce economic losses during hot periods. Where active temperature control is feasible, engineering and economic analyses indicate that it can be cost-effective when carefully designed. Energy-modelling of a New Zealand land-based abalone farm found that temperature control using a semi-closed conditioning system with heat pumps can enhance growth and reduce summer mortality, but poor design may create very high energy demand; the study shows that plant design strongly influences operating costs (Jayatissa et al., 2002). For broodstock in cold regions, switching from flow-through heated systems to a simple closed recirculating system reduced electric power consumption for heating to about one-seventh while maintaining or even improving gonad development, showing that recirculation with heat retention can greatly cut energy costs without sacrificing biological performance (Matsumoto and Maeda, 2021).

8 Management Strategies for Temperature Regulation in Abalone Aquaculture

Technological solutions that actively regulate water temperature are central to stabilizing production in intensive abalone systems. In cold regions, Japanese hatcheries that induce gonadal maturation of *Haliotis discus hannai* by heating seawater can substantially cut energy costs by shifting from flow-through to simple closed recirculating systems that reuse warmed water, reducing power consumption for heating to about one-seventh while maintaining water quality and normal gonad development. More advanced engineering approaches in recirculating aquaculture workshops use computational fluid dynamics to simulate heat exchange between indoor air and water, allowing accurate estimation of cooling loads and optimization of ground-source heat pump units, which reduces over-design and investment in temperature-control equipment. Thermal models and low-cost control hardware further refine facility operation. Heat-balance modelling for recirculating aquaculture systems has produced user-friendly tools capable of predicting hourly to annual heating and cooling requirements, solar radiation and water temperature, with realistic accuracy relative to measured tank temperatures; these tools support design choices that minimize heating costs while maintaining optimal thermal regimes. Experimental work on small recirculating tank systems shows that inexpensive in-situ coil heat exchangers, coupled to computer-controlled chillers and heaters, can impose desired temperature regimes efficiently, illustrating a practical route for fine-scale temperature management in multi-tank abalone facilities.

Stocking density interacts strongly with temperature and water quality, so coordinated management is necessary to sustain growth and survival. In land-based recirculating systems, *Haliotis discus hannai* stocked at 600-1000 ind m^{-2} showed significantly higher survival, specific growth rate and food intake than abalone held at 1500 ind m^{-2}, with the high-density group exhibiting elevated moisture, lactic acid and antioxidant enzyme expression, indicating heightened metabolic and oxidative stress despite identical environmental conditions. complementary studies under flow-through conditions show that at 1200-1500 ind/m^2, glycolytic and anaerobic enzymes (hexokinase, pyruvate kinase, lactate dehydrogenase) are upregulated and more energy is diverted to resisting oxidative damage, leaving little energy for growth, whereas 900 ind/m^2 yields the highest survival and energy accumulation for growth and is recommended as an upper practical density. Optimizing density also depends on culture system and exposure to open-water temperature fluctuations. On an offshore mechanized platform, increasing coverage from 20 to 50% of cage surface area reduced survival and growth of abalone over 240 days, even though food was adequate, while well-chosen densities and diets on this offshore system improved growth relative to a traditional nearshore model and reduced pressure on warmer, more variable coastal environments. Long-term cage trials with *Haliotis* asinina similarly found an inverse relationship between growth and density but little effect on survival, highlighting that economic choices must balance individual growth rates against total biomass gain, with moderate densities often providing the most favourable trade-off under given environmental conditions.

Building climate-resilient abalone farming systems requires integrating genetic, technological and ecosystem-based strategies to buffer increasing temperature variability and extremes. Reviews of aquaculture adaptation emphasize selective breeding, species diversification, and advanced systems such as recirculating aquaculture, aquaponics and integrated multi-trophic aquaculture (IMTA) as core climate-resilient approaches that enhance adaptive capacity to warming, acidification and extreme weather while supporting sustained production. In an abalone-specific context,

comparative work on northern and southern *Haliotis discus hannai* populations shows that long-term exposure and selection in warmer waters produces domesticated stocks with enhanced thermal tolerance and superior regulation of carbohydrate and amino-acid metabolism, demonstrating that breeding and translocation programs can deliberately cultivate heat-tolerant lines for deployment in warming regions. Genomic tools are emerging as powerful levers to accelerate thermal adaptation. Quantitative genetic and genomic selection work on *Pacific abalone* reports moderate heritability (0.35-0.42) for heat-tolerance traits and demonstrates that genomic selection models can predict heat tolerance with high accuracy, identifying specific SNP markers and candidate genes that can be used in marker-assisted breeding programs to improve resilience to marine heatwaves. Ecosystem-based designs like abalone-seaweed co-culture further enhance climate resilience by biologically modifying water conditions: in juvenile red abalone, IMTA with the red seaweed dulse elevated pH under simulated ocean acidification, producing faster growth, better condition and stronger shells, and thereby "shepherding" juveniles through their most vulnerable life stage despite deteriorating external seawater quality.

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