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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).

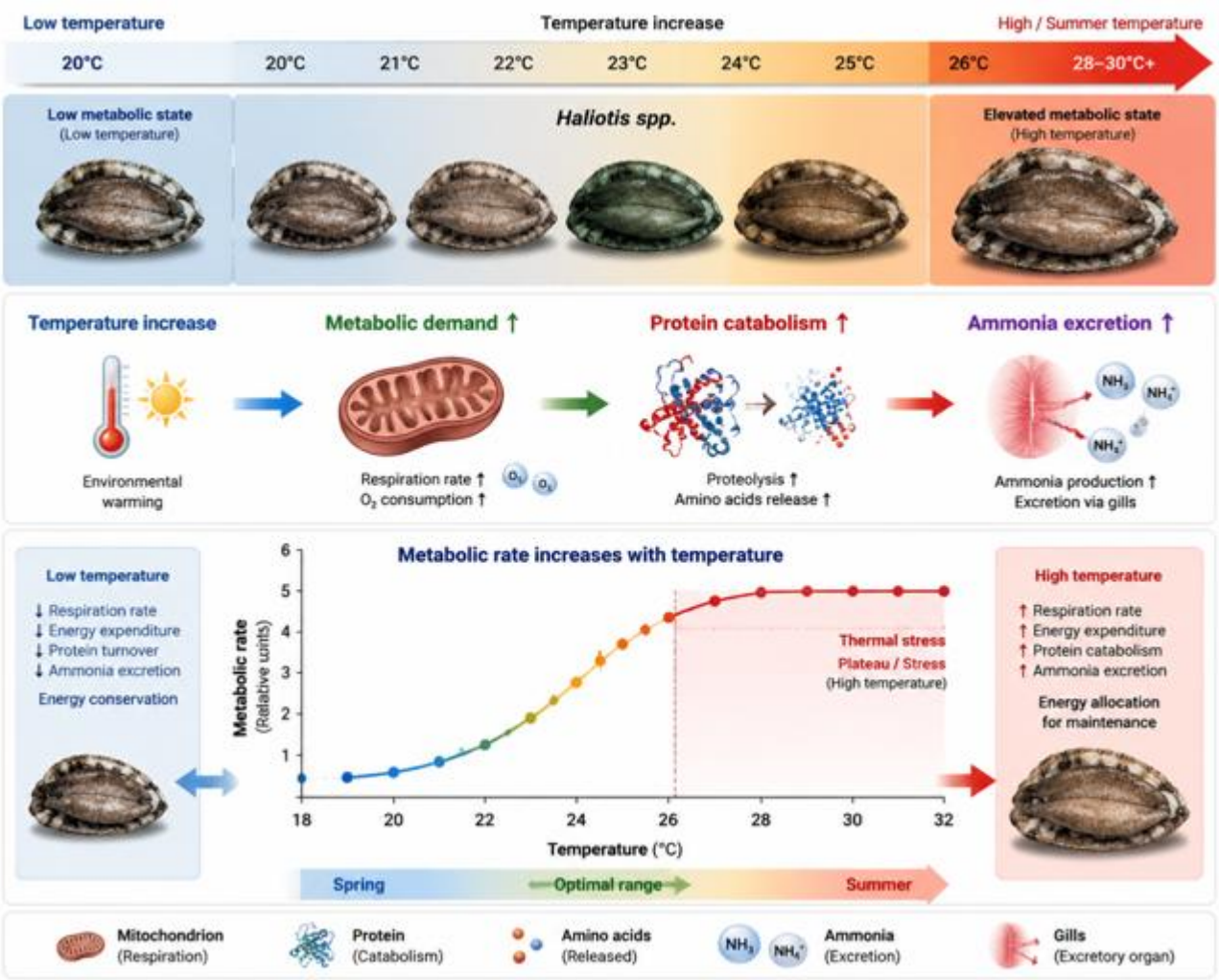

Figure 1 Temperature-driven metabolic regulation in *Haliotis* spp.

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.

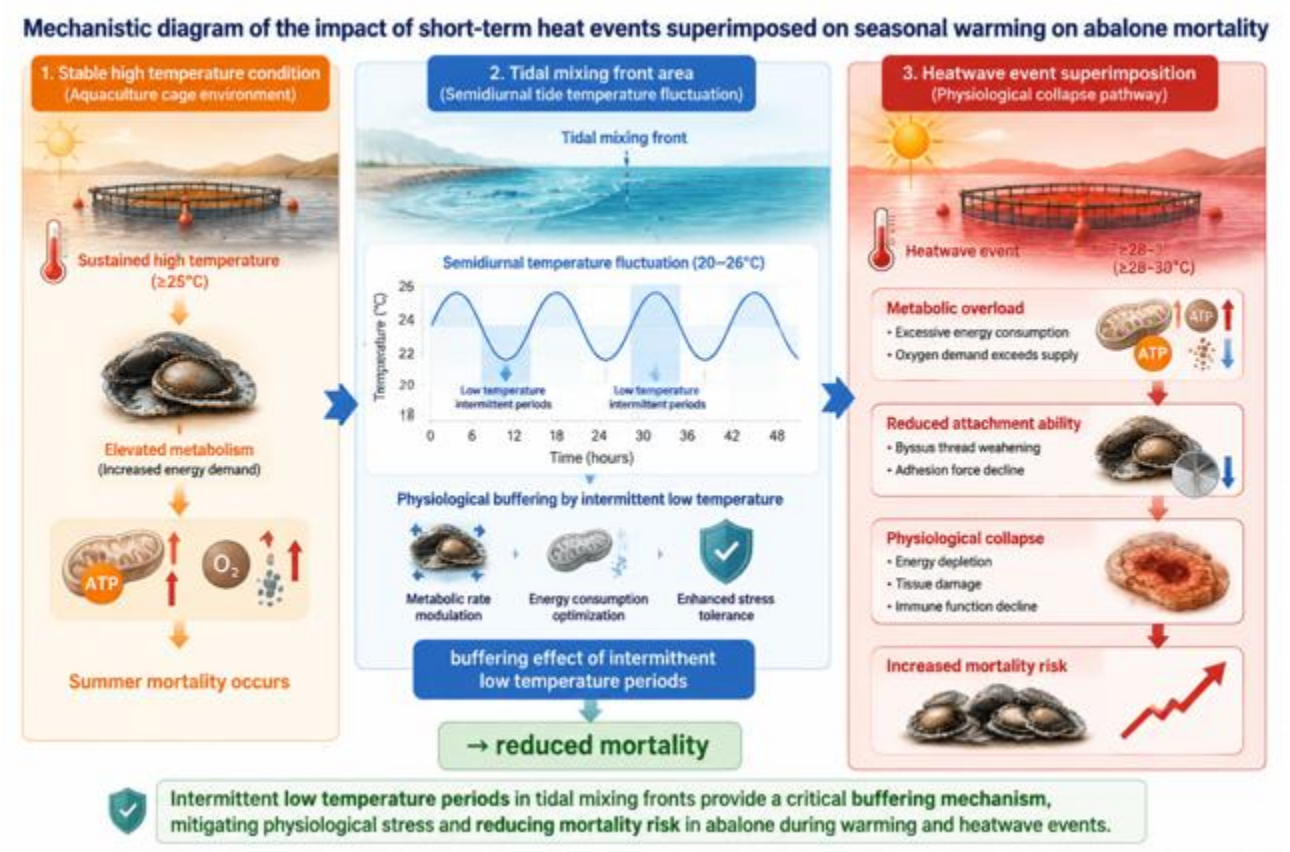

Figure 2 Buffering effects of short-term temperature fluctuations on summer mortality in *Haliotis* spp.

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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Effects of Environmental Factors on the Health Status of Turbot (*Scophthalmus maximus*)

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Abstract As an important marine aquaculture species, the health status of the turbot (*Scophthalmus maximus*) is significantly influenced by various environmental factors during intensive farming. This paper systematically reviews the mechanisms by which key environmental factors-such as temperature, salinity, dissolved oxygen, and water quality-affect the physiological homeostasis, immune function, and disease susceptibility of turbot. The results indicate that temperature fluctuations can alter immune responses by inducing metabolic imbalances and changes in heat shock protein expression, thereby increasing susceptibility to pathogens. Salinity variations disrupt osmoregulatory systems, triggering stress responses and compromising disease resistance. Insufficient dissolved oxygen and the accumulation of ammonia-nitrogen lead to chronic stress and tissue damage, exacerbating health risks. Furthermore, environmental stressors enhance the pathogenicity of bacteria (such as **Vibrio** spp.), further promoting disease outbreaks. In high-density aquaculture systems, the coupled effects of multiple factors significantly amplify these health risks. Based on this analysis, the paper proposes strategies for environmental monitoring and integrated regulation to mitigate the adverse effects of environmental stress on turbot health and to enhance the stability and productivity of aquaculture systems.

Keywords Turbot; Environmental factors; Temperature stress; Osmoregulation; Disease outbreak

1 Introduction

Turbot aquaculture has become an important component of marine finfish production, driven both by declining wild stocks and by the species' favorable farming traits. Wild turbot catches have generally decreased since the mid-1990s, and aquaculture production has exceeded capture production since 2002, while the species remains valued for rapid growth, high survival, and efficient feed conversion. Over the past several decades, these attributes have supported the industrial development of turbot farming in Europe, and large-scale expansion in China has made turbot one of the world's most important cultivated flatfish species, with annual Chinese production reported above 60,000 tons in the first two decades after introduction (Fernández-González et al., 2022).

At the same time, the success of turbot culture depends strongly on environmental suitability, because this cold-water marine species performs best within relatively narrow physicochemical ranges. In European production systems, water temperatures of about 15°C-19°C and salinity of 25-35 psu are identified as key conditions for successful farming, highlighting the central role of site quality and water management in production outcomes (Fernández-González et al., 2022). More broadly across fishes, temperature, pH, salinity, and dissolved oxygen shape physiology, metabolism, behavior, and survival, with salinity shifts altering energy allocation and gill function, and low dissolved oxygen reducing growth, reproduction, and disease resistance (Mariu et al., 2023).

For marine fish, environmental factors are not only determinants of growth performance but also major regulators of stress and health status. Temperature increases can act as a direct physiological stressor, especially in ectothermic species approaching their upper thermal tolerance limits, and warming can also worsen oxygen-related constraints and broader population-level vulnerability (Alfonso et al., 2020). Turbot-specific studies show the same pattern at the organismal level: high stocking density suppresses growth, elevates cortisol and glucose, and weakens skin immune defenses, while elevated ammonia activates stress pathways and inhibits humoral immunity, indicating that environmental deterioration can rapidly translate into impaired welfare and disease susceptibility.

These concerns are especially relevant because environmental stress in turbot often operates through interacting physiological mechanisms rather than through simple single-factor effects. Elevated temperature in farmed turbot has been linked to increased disease-associated mortality above 20°C and to molecular signatures of oxidative stress and metabolic disturbance under pathogen challenge, while low salinity stress disrupts liver lipid metabolism and depresses key metabolic pathways (Liu et al., 2020). Against this background, the objective of this review is to synthesize current knowledge on how major environmental factors influence the health status of turbot, with emphasis on stress physiology, immune competence, and metabolic regulation. Such a synthesis is significant for improving environmental control in intensive culture systems, guiding health-oriented farm management, and identifying priorities for future research as climate change and production intensification continue to reshape the conditions under which turbot are farmed (Mariu et al., 2023).

2 Biological and Physiological Characteristics of Turbot (*Scophthalmus maximus*)

2.1 Growth traits and ecological adaptation

Turbot is a demersal flatfish distributed from the Northeast Atlantic to the Mediterranean, Baltic, and Black seas, and its life history reflects strong adaptation to benthic habitats. Larvae retain high dispersal potential through a pelagic phase, whereas postlarvae, juveniles, and adults are relatively sedentary, a combination that links local habitat specialization with broader population connectivity. Genomic evidence further indicates that ecological adaptation in this species has been shaped by environmental selection, with temperature and salinity emerging as major drivers and with candidate genes associated with osmoregulation, growth, and disease resistance identified in selected genomic regions.

The species also shows marked physiological and production-related variation in growth. Whole-genome analysis links turbot's adaptation to demersal and relatively cold environments to selection on genes involved in vision and membrane lipid metabolism, and reports sustained growth across approximately 13°C-20°C, indicating capacity to perform under cool and fluctuating thermal conditions. At the individual level, growth is strongly structured by sex and metabolic phenotype: females ultimately outgrow males under most thermal regimes, while fast-growing fish show up-regulation of anaerobic glycolytic pathways in white muscle, consistent with a higher metabolic rate supporting rapid somatic growth.

2.2 Immune system and stress response mechanisms

In turbot, stress responses involve endocrine activation together with tissue-specific immune modulation. Acute handling stress elevates cortisol and plasma K^+ after both aerial exposure and net confinement, but unlike the canonical response described for many other teleosts, turbot shows little or no parallel rise in plasma glucose, suggesting a distinctive stress physiology. Chronic crowding likewise acts as a potent stressor: high stocking density suppresses growth, increases plasma cortisol and glucose, and reduces mucus immune activities such as lysozyme, alkaline phosphatase, and esterase, indicating weakened barrier defense at the skin surface (Yang et al., 2020).

Environmental insults also connect the hypothalamic-pituitary-interrenal axis with oxidative stress and immune suppression. Under elevated ammonia exposure, juvenile turbot show increased CRH, ACTH, and cortisol together with reduced lysozyme, complement factors, and IgM, while liver antioxidant responses and heat-shock protein expression rise alongside lipid peroxidation, consistent with stress-induced immune inhibition and oxidative damage. Thermal stress appears to alter disease resistance through a related mechanism: at 21°C, challenged fish exhibit enhanced neutrophil-associated responses, sustained myeloperoxidase-linked oxidative stress, and disturbed NADPH and glucose metabolism, changes proposed to underlie thermo-linked epizootic risk in turbot culture.

2.3 Temperature and salinity tolerance ranges

Temperature and salinity jointly determine performance in juvenile turbot, and their interaction is more informative than either factor alone. In a three-month rearing study, growth, feed intake, and feed conversion efficiency were highest at 15‰ and lowest at full-strength seawater, with the overall optimal growth combination estimated at about 21.8°C and 18.5‰ (Jia et al., 2020). Osmoregulatory measurements support the same pattern: gill Na^+, K^+-ATPase activity, plasma chloride, and osmolality were lowest at intermediate salinity, implying reduced energetic costs of ion regulation under brackish to moderately saline conditions.

Tolerance limits nevertheless vary with life stage and endpoint. Sudden-change experiments in juveniles estimated incipient lethal limits at 7.06°C-26.54°C and 16.05-37.76 salinity, with highest short-term survival around 15°C-18°C and salinity 28-32, showing that survival tolerance is broader than the optimum for growth. Reproductive stages are more constrained: in Baltic turbot, fertilization success and viable hatch decline sharply below 7 psu, while egg survival is highest at 12°C-18°C and lower at 9°C and 21°C, indicating that successful reproduction near the species' brackish distribution limit depends on a narrower hydrographic window than juvenile persistence (Yang et al., 2020).

3 Key Environmental Temperature Effects on Health

3.1 Thermal stress and metabolic imbalance

Thermal stress rapidly disrupts energy metabolism in turbot and forces a shift toward compensatory catabolic pathways. In kidney tissue, exposure to 25°C-28°C increased cortisol, creatinine, *hsp70*, and *hsp90*, while also upregulating enzymes linked to aerobic metabolism and gluconeogenesis, including SDH, FBPase, MDH, cPEPCK, and G6Pase, indicating that maintenance of energy supply under heat load depends on metabolic reprogramming rather than simple metabolic depression (Yang et al., 2020). Consistent with this, integrated metabolome-transcriptome analysis showed that heat stress significantly affected pathways involved in steroid hormone biosynthesis, glycerophospholipid metabolism, sphingolipid metabolism, glycerolipid metabolism, and unsaturated fatty acid biosynthesis, suggesting that lipid homeostasis is also extensively remodeled during thermal challenge (Zhao et al., 2021).

At the whole-animal level, acute hyperthermal exposure at 27°C elevated serum cortisol, glucose, and respiratory frequency during the early stress phase, while hepatic glycogen, CAT, and GPx progressively declined and malondialdehyde increased, indicating rising oxidative cost and depletion of metabolic reserves as stress duration lengthened (Jia et al., 2020). Broader transcriptomic evidence supports this interpretation by showing that heat stress in turbot kidney enriches pathways related to fat metabolism, insulin signaling, apoptosis, FOXO, Jak-STAT, and P53 signaling, with hub genes such as AKT3, PIK3r2, and mdm2 implicated in coordinating the balance between metabolic adjustment and cellular injury under elevated temperature.

3.2 Heat shock protein (HSP) expression and immune modulation

Heat shock proteins are among the most responsive molecular indicators of temperature stress in turbot, but their regulation is tissue-specific and linked to broader stress physiology. Under rapid cooling from 18°C to 1°C, red and white blood cell counts and hemoglobin fell significantly, while cortisol, cholesterol, and triglycerides increased; in parallel, *hsp70* and *hsp90* expression changed across tissues, and the authors identified 8°C-5°C as a critical low-temperature stress zone for aquaculture management. Under heat exposure, *hsp70* and *hsp90* transcripts in liver increased significantly within 6-12 h, accompanying early endocrine disturbance and the onset of hepatocyte apoptosis, which supports the view that HSP induction forms part of an acute protective response that is activated before prolonged thermal damage becomes established (Figure 1) (Jia et al., 2020).

Mechanistically, heat-induced HSP regulation in turbot is not merely descriptive but has defined signaling features. In turbot kidney cells, heat stress activated ERK1/2 and HSF1 and induced *hsp90* expression, while ERK inhibition attenuated this response, identifying an ERK-HSF1-dependent pathway in the cellular heat shock response (Yang et al., 2020). At the genome-wide level, 16 *hsp70* genes have been identified in turbot, and several members-especially *hspa1a*, *hspa1b*, and *hspa5*-show strong responses across heat, salinity, parasitic, bacterial, and viral stress datasets, indicating that the HSP network participates not only in thermal protection but also in immune modulation across diverse environmental and infectious challenges (Zheng et al., 2023).

3.3 Temperature-related disease susceptibility patterns

Temperature strongly shapes disease susceptibility in turbot by altering both host defense capacity and pathogen performance. In megalocytivirus challenge experiments, fish held at 14°C-18°C showed undetectable or moderate viral replication and no mortality, whereas fish held at 20°C-24°C showed robust viral replication and 100% mortality; furthermore, shifting temperature downward during infection improved survival, while upward shifts

worsened outcomes (Jia et al., 2020). These results indicate that relatively small increases above the lower culture range can decisively transform infection from controlled to lethal, making temperature management a central component of viral disease prevention.

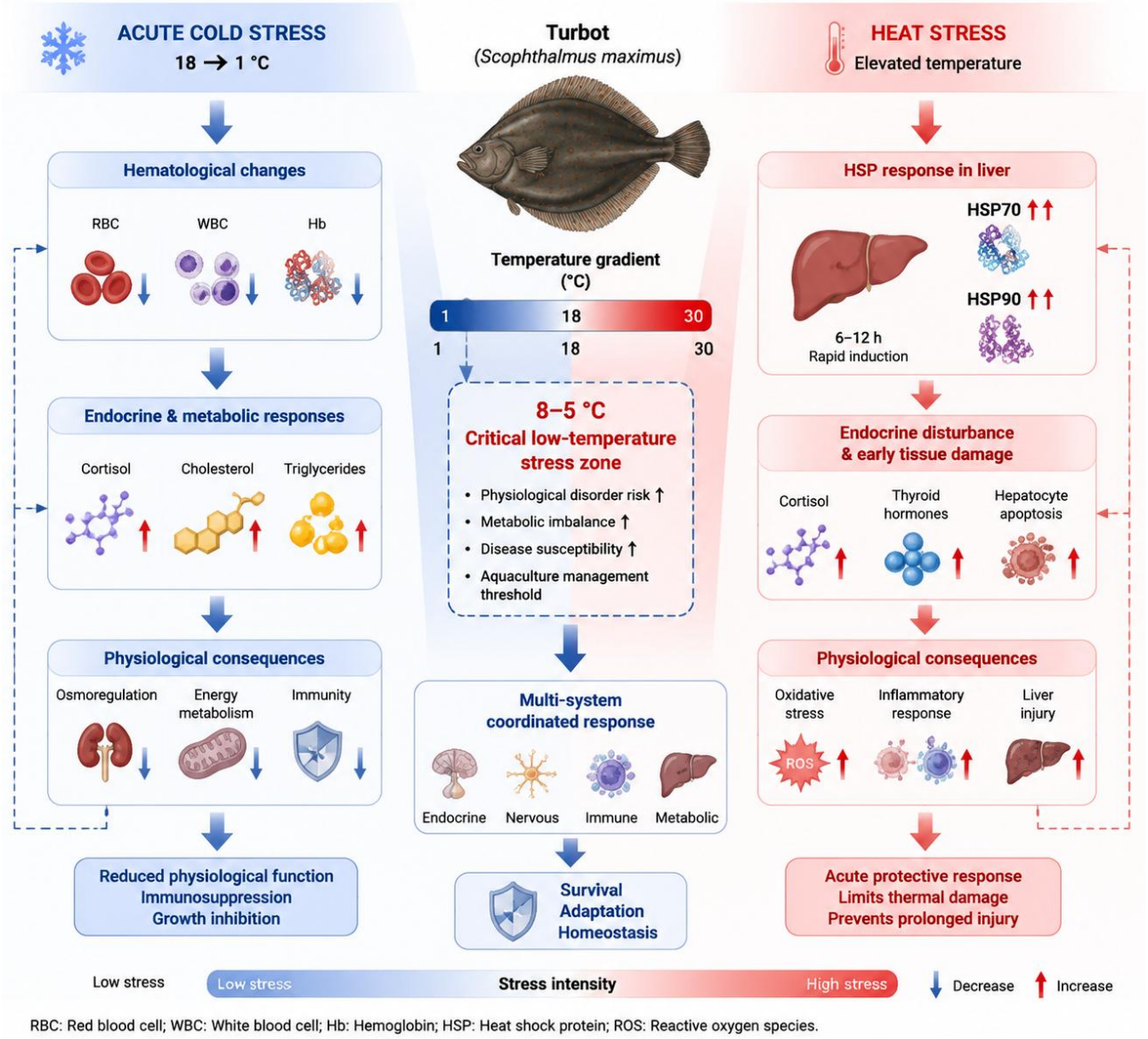

Figure 1 Integrated physiological and molecular stress responses of turbot under acute cold and heat exposure, highlighting hematological changes, endocrine disruption, and HSP70/HSP90 regulation

Evidence from pathogen-mimic challenge further suggests that high temperature can increase disease risk even when immune activity is stimulated rather than suppressed. Integrated transcriptomic and proteomic analyses showed that elevated temperature enhanced neutrophil-mediated responses but also intensified MPO-associated oxidative stress and disturbed NADPH and glucose metabolism, a combination proposed to contribute to thermo-linked epizootics in turbot (Liu et al., 2020). Related work on high water temperature and skin mucus immunity found significant temperature-dependent changes in immune-related factors at the mucosal surface, supporting the view that warming reshapes frontline defense systems as well as systemic stress pathways.

4 Salinity and Osmoregulatory Stress

4.1 Osmoregulation mechanisms in turbot

Turbot osmoregulation depends on coordinated responses across the gill, kidney, and other regulatory tissues, with ion transport and signaling pathways forming the core of adaptation to hypoosmotic challenge. Kidney

transcriptomics under salinity 5 versus 30 showed that inorganic ion channels and transporters, mineral absorption, and bile secretion contribute to iono-osmoregulation and cell-volume regulation, while tissue-specific analysis identified the kidney, gill, and spleen as major osmoregulatory organs. Complementary work further showed that low salinity activates PI3K-AKT signaling in osmoregulatory organs and that pathway inhibition suppresses ion-channel gene expression, indicating that signal transduction positively regulates ion transport during osmotic adjustment (Cui et al., 2020).

Hormonal and osmolyte-mediated regulation also plays a central role in salinity adaptation. Under low-salt stress, pituitary PRL expression and PRLR expression in gill and kidney increased and peaked at 12 h, while long-term low-salinity exposure maintained especially high PRLR expression in the gill, suggesting that PRL signaling is important in sustained hypoosmotic regulation (Liu et al., 2020). In parallel, the myo-inositol biosynthesis pathway showed adaptive expression with a 12 h turning point across tissues, and RNAi knockdown weakened gill osmotic regulation and shortened survival under salinity stress, showing that organic osmolyte metabolism is a functional component of turbot osmoregulation.

4.2 Effects of salinity fluctuations on physiological stability

Salinity fluctuations affect physiological stability by changing the energetic cost of ion regulation and altering core blood and enzyme indicators. In juvenile turbot reared for three months across 15, 25, and 33.5‰, gill Na+, K+-ATPase activity, plasma chloride, and osmolality were lowest at 15‰, and estimated optima for minimum osmoregulatory load clustered around intermediate salinities, supporting the view that moderate salinity reduces the energy expenditure required for homeostasis (Liu et al., 2020). This energetic dimension is reinforced at the molecular level by evidence that salinity challenge changes AMPK α1/α2 expression in gill in a time- and salinity-dependent manner and that AMPK expression is positively correlated with Na+, K+-ATPase activity, linking salinity stress directly to cellular energy sensing.

When salinity departs too far from normal seawater, stability is maintained only through broader metabolic and endocrine compensation. Low salinity caused major liver transcriptional changes, with 826 differentially expressed genes enriched in energy metabolism and especially lipid metabolism, and serum triglycerides decreased over time in freshwater exposure, indicating metabolic disturbance rather than neutral acclimation (Liu et al., 2020). Over longer exposure, low salinity at 10 ppt remodeled circadian organization of physiological markers by shifting or replacing normal daily rhythms of T3, T4, and ALT without clear oxidative damage, suggesting that chronic hyposmotic stress can preserve short-term balance but only by reorganizing endocrine and metabolic timing (Liu et al., 2026).

4.3 Interaction between salinity stress and pathogen infection

Salinity stress interacts with infection largely through its effects on host immunity and resistance rather than through direct pathogen measurements alone. In juveniles reared at 8, 20, 32, and 40, fish at salinity 20 had the highest 4-day LD50 after *Vibrio anguillarum* challenge and also showed the highest lysozyme, complement, and phagocytic activity, whereas immunity was poorest at salinity 40, indicating that intermediate salinity supports stronger disease resistance than more extreme salinity conditions. Additional response-surface analysis showed that salinity significantly shapes expression of immune markers such as *hsp70* and IgM in liver and kidney, with a significant temperature-salinity interaction for kidney IgM, supporting the conclusion that salinity modifies immune competence in a tissue-specific way (Cui et al., 2020).

Mechanistic studies suggest that improved osmotic capacity can indirectly strengthen resistance to salinity-associated health decline. Dietary or immersion myo-inositol increased gill myo-inositol content, extended survival under salinity stress, and enhanced osmoregulatory, antioxidant, and immune-related functions, with steroid-associated pathways occupying a central place in this response (Cui et al., 2020). Consistently, dietary myo-inositol also prolonged survival under low salinity by modulating cortisol synthesis, increasing Na+-K+-ATPase activity and ion-channel gene expression, whereas suppression of cortisol eliminated these benefits, indicating that endocrine support for osmoregulation can help buffer the immune and survival costs that accompany salinity stress.

5 Dissolved Oxygen and Water Quality Impacts

5.1 Hypoxia-induced physiological and behavioral changes

Turbot is notably sensitive to reduced dissolved oxygen, with measurable behavioral disturbance appearing before lethal thresholds are reached. During progressive hypoxia, abnormal swimming behavior was observed when dissolved oxygen fell below 5 mg/L, respiration frequency increased at the critical oxygen tension, and loss of equilibrium occurred near 1.30 mg/L; related work identified a critical oxygen tension around 3.34 mg/L and showed that turbots under severe hypoxia first respond through increased ventilation amplitude and frequency to maintain oxygen uptake (Maxime et al., 2000). This initial compensatory phase reflects a relatively strong short-term regulatory capacity, but it does not prevent endocrine and metabolic stress as oxygen availability continues to decline. At low oxygen tension, plasma cortisol, glucose, and lactate increase markedly, and severe hypoxia triggers rises in adrenaline and noradrenaline together with reduced arterial oxygen partial pressure, indicating activation of both the stress axis and anaerobic metabolism (Jia et al., 2021).

Longer hypoxic exposure shifts the response from acute compensation to impaired growth and tissue-level remodeling. Under chronic hypoxia at about 3.5 mg/L for 8 weeks, turbot showed reduced digestibility, feed efficiency, weight gain, and body indices, along with poorer muscle texture, lower nutrient content, and reduced myofiber number, indicating that oxygen shortage depresses both production performance and flesh quality (Guo et al., 2026). Similar long-term exposure elevated plasma cortisol and glucose, increased glycolytic and lipolytic enzyme activities, altered gill morphology, and upregulated *hif-1α*, *hif-2α*, and *hif-3α*, suggesting that chronic hypoxia induces coordinated endocrine, metabolic, and branchial adjustments to sustain gas exchange and energy balance (Jia et al., 2021).

5.2 Ammonia, nitrite, and toxic metabolite accumulation

Nitrogenous wastes are major toxicants in intensive turbot culture, and both ammonia and nitrite disrupt physiological homeostasis within short exposure periods. High ammonia exposure elevated CRH, ACTH, and cortisol while reducing GH, lysozyme, complement factors, and IgM, demonstrating simultaneous activation of the hypothalamic-pituitary-interrenal axis and suppression of humoral immunity. Nitrite caused a partly overlapping but distinct syndrome: at 0.4-0.8 mM, it increased GPT, GOT, ALP, *c3*, and C4, reduced IgM and lysozyme, and upregulated gill *hsp70*, *hsp90*, TLR-3, *tnf-α*, and *il-1β*, indicating blood physiological dysfunction together with inflammatory and immune disturbance (Jia et al., 2024).

The toxic effects of these metabolites also extend to oxidative damage, ion imbalance, and reduced oxygen transport. In ammonia-exposed fish, liver SOD and CAT activities, HSP expression, and MDA increased while GSH and IGF-1 decreased, supporting a mechanism involving oxidative stress and impaired growth regulation. Nitrite and nitrate further compromise oxygen-carrying capacity: nitrite raised methemoglobin, cortisol, glucose, and K+ while lowering hemoglobin and Na+, whereas chronic nitrate exposure increased plasma NO3-, NO2-, methemoglobin, cortisol, glucose, lactate, and K+ and decreased Hb, Na+, and Cl-, indicating hypoxic stress combined with osmoregulatory and metabolic disruption (Yu et al., 2021).

5.3 Water quality deterioration and chronic stress effects

Beyond acute toxicants, chronic deterioration of water quality in recirculating or high-density systems imposes persistent stress that reduces growth and damages multiple organs. Elevated nitrate over 60 days reduced survival and growth, caused dose-dependent gill and liver histopathology, lowered hemoglobin, increased methemoglobin, and dysregulated the GH/IGF-1, thyroid, and HPI axes, showing that nitrate acts as a chronic systemic stressor rather than a benign end-product of nitrification (Yu et al., 2021). Chronic nitrate exposure also injured the intestine by causing microvillus atrophy and lamina propria necrosis, downregulated tight-junction and mucin genes, and shifted the microbiota toward lower intrinsic flora and more potential pathogens, indicating weakened barrier function and long-term health deterioration (Yu et al., 2020).

Other chronic water-quality stressors in RAS show similarly broad impacts. Prolonged CO_2 exposure reduced specific growth rate, increased feed conversion ratio, damaged gill, liver, and intestinal tissues, and altered plasma

HCO3-, Na+, and Cl- as well as osmoregulatory and acid-base genes, indicating sustained disturbance of ion balance and buffering physiology even at relatively low CO_2 concentrations (Guo et al., 2023). Chronic handling or crowding stress also amplifies these effects at the whole-animal level: repeated handling elevated cortisol and progressively depressed innate immune indicators, while high-density exposure combined with ammonia intensified Na+ imbalance, Na+/K+-ATPase activity, and pro-inflammatory and heat-shock gene expression, showing that poor water quality and husbandry stress often interact rather than act in isolation.

6 Pathogen Dynamics under Environmental Stress

6.1 Bacterial infections

Bacterial disease is a persistent constraint in turbot aquaculture, and *Vibrio* spp. have been especially prominent across larval and grow-out systems. Early reports identified *Vibrio*sis as a common problem in turbot production and documented the involvement of several taxa, including *Vibrio anguillarum* serogroups O1, O2a, and O2b, as well as members of the *V. splendidus*/*pelagius* group. Farm-level microbiological surveys similarly found that *Vibrio* spp. were among the most prevalent bacteria recovered from diseased turbot, although lesion type could not always be linked to a single bacterial species.

More specific evidence shows that some *Vibrio* isolates are highly virulent under culture conditions. A *Vibrio pelagius* strain recovered from larval mass mortality was highly pathogenic to larvae and post-larvae, with an LD50 below 5 bacteria mL^-1 in larvae, and the isolate was also able to grow in sterile seawater at room temperature or 15°C, indicating both strong host pathogenicity and environmental persistence. In parallel, *Aeromonas salmonicida* is an important cause of furunculosis-related losses in turbot farming, and infection triggers early up-regulation of pro-inflammatory and innate immune genes such as *tnf-α*, *il-1β*, *il-10*, and *c3*, showing that even early-stage bacterial challenge rapidly perturbs host immune homeostasis (Fajardo et al., 2023).

6.2 Viral and parasitic outbreaks

Viral diseases in turbot range from larval neurologic syndromes to emerging hemorrhagic conditions in grow-out fish. A picornavirus-like agent was associated with encephalomyelitis in turbot larvae, with large numbers of virus particles observed in the brain and medulla and with outbreaks ending in extremely heavy, ultimately complete mortality in affected batches. More recently, turbot acute hemorrhage disease in China was linked to a novel circovirus, and diseased stocks showed rapid spread, mortality exceeding 90% within one to two weeks, and increasing viral copy numbers after experimental infection (Figure 2) (Jiang et al., 2024).

Parasitic diseases are also major components of pathogen dynamics in stressed turbot populations. *Enteromyxum scophthalmi* causes a severe enteric disease characterized by cachexia, high morbidity, and mortality, while early infection is marked by interferon-related responses together with down-regulation of complement and acute-phase genes, suggesting active immune evasion during colonization (Spinos et al., 2024). Likewise, *Philasterides dicentrarchi* causes scuticociliatosis with systemic tissue invasion, including severe encephalitis, hepatic necrosis, branchial lesions, and muscular degeneration, confirming that parasitic outbreaks in turbot can progress beyond surface infestation to multisystemic disease.

6.3 Environmental drivers of disease transmission and virulence

Environmental stress does not simply weaken the host; it also changes transmission opportunity and pathogen virulence. A classic fisheries disease framework showed that infectious outbreaks arise when susceptible fish encounter virulent pathogens under stress caused by temperature, eutrophication, sewage, metabolic wastes, industrial pollution, or pesticides (Spinos et al., 2024). In turbot specifically, simultaneous environmental and biological stress can act synergistically: low water depth elevated cortisol and metabolic disturbance, and the additional presence of *A. salmonicida* or *P. dicentrarch*i under these conditions further amplified several stress responses.

Temperature is one of the clearest environmental drivers of bacterial virulence and outbreak timing. In fish-pathogenic bacteria, temperature regulates virulence gene expression, and in *Aeromonas hydrophila* lower host-

relevant temperatures enhanced production of extracellular virulence factors and type III secretion-associated proteins, illustrating how virulence can increase under ectothermic infection conditions. Field and epidemiological observations support the same pattern in turbot systems: ulcerative disease outbreaks in juvenile turbot began after water temperature rose above 20°C, while broader aquaculture case studies have linked increasing temperature and salinity, especially when combined with reduced dissolved oxygen, to higher occurrence of *Vibrio*sis and other infectious diseases (Spinos et al., 2024).

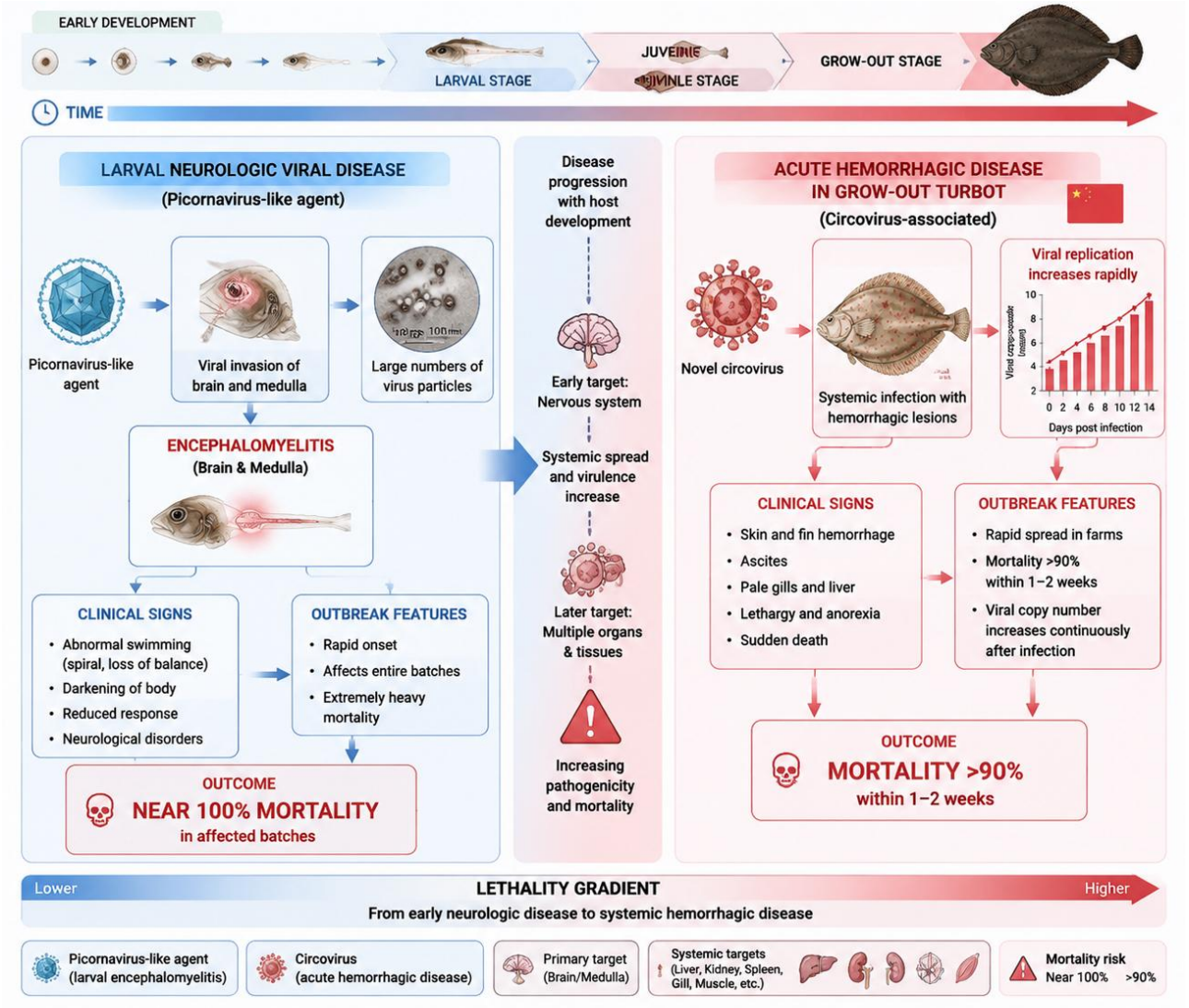

Figure 2 Progression of viral diseases in turbot from larval encephalomyelitis associated with picornavirus-like agents to acute hemorrhagic disease caused by a novel circovirus in grow-out stages

7 Feeding Environment and Nutritional Immunity

7.1 Temperature-dependent feeding behavior and digestion efficiency

As an ectothermic fish, turbot shows feeding and digestive responses that are tightly regulated by temperature, but these responses are not linear across the full thermal range. General fish evidence shows that temperature affects both feeding motivation and the capacity to digest and absorb nutrients, while turbot-specific trials indicate that feed intake increases from 14 to 18°C but declines significantly at 21°C under high-density recirculating conditions, suggesting that warming beyond the optimal range reduces appetite rather than continuously stimulating it. This pattern is consistent with the view that thermal effects on feeding are species-specific and depend on exposure intensity and duration, which is particularly relevant for a cold-water species such as turbot (Volkoff and Rønnestad, 2020).

Temperature also alters digestive efficiency by changing enzyme activity, gut processing, and the energetic scope available for postprandial metabolism. In fish generally, digestibility usually declines outside the optimal thermal window because digestive enzyme activities are temperature sensitive, and in turbot, pepsin activity increases from 14°C to 18°C before dropping sharply at 21°C, identifying 16°C-18°C as the practical optimum for feed intake, growth, and digestive performance in larger fish (Volkoff and Rønnestad, 2020). Older radiographic work further showed that gastric emptying time in turbot decreases as temperature rises, indicating faster meal processing at warmer temperatures, but this benefit should be interpreted together with the decline in appetite and enzyme performance once temperatures exceed the optimal range.

7.2 Nutritional regulation of immune competence

Nutritional status is a direct regulator of immune competence in turbot, because both adequate baseline nutrition and targeted supplementation can shape innate and adaptive defense functions. Broad aquaculture reviews agree that balanced nutrient supply is required for efficient host defense and that specific nutrients supplied above minimum requirement can improve fish health and disease resistance. In turbot, this principle is supported by vitamin D3 studies showing that dietary supplementation reduced mortality and spleen bacterial load after *Edwardsiella tarda* infection, while also elevating serum lysozyme activity, haemocyte reactive oxygen species production, and macrophage bactericidal capacity (Liu et al., 2021).

Other micronutrients similarly regulate turbot immunity through antioxidant protection and immune-gene modulation. Dietary vitamin E supplementation increased growth, lysozyme activity, phagocytic index, superoxide dismutase activity, and the expression of immune-related genes including *c3*, *tnf-α*, and *il-1β*, with the best overall response reported at 480 mg kg^-1. Vitamin C supplementation also enhanced non-specific immunity in juvenile turbot, particularly by increasing serum lysozyme and phagocytic capacity, whereas both deficient antioxidant supply and oxidized dietary lipid exposure suppressed head-kidney phagocyte function and increased mortality after *Vibrio anguillarum* challenge.

7.3 Feed quality deterioration under environmental stress

Environmental stress can degrade feed quality before ingestion, thereby weakening nutritional value and increasing toxicological risk. Storage studies show that humidity and temperature strongly influence the formation of mycotoxins in compounded fish feeds, and even short-term exposure to unsuitable storage conditions can deteriorate feed quality and promote fungal contamination. Warm, humid storage is particularly problematic because ochratoxin A was detected after treatment at about 25°C and >60% relative humidity, demonstrating how rapidly hazardous contaminants can develop in stored aquafeeds (Pietsch et al., 2020).

The biological consequences of feed deterioration extend beyond reduced nutrient density to impaired immunity and poorer production performance. Reviews on aquafeed contamination note that plant-based ingredients such as maize and oilseeds are favorable substrates for mycotoxigenic fungi and that mycotoxin exposure in fish is associated with reduced weight gain, poorer feed conversion, immune impairment, higher mortality, and possible carryover risks along the food chain. In turbot specifically, nutritionally damaged feed can also act through oxidative deterioration: fish given oxidized fish oil with antioxidant deficiency showed depressed phagocyte chemiluminescent response and higher mortality after bacterial challenge, confirming that environmentally induced feed spoilage can translate directly into reduced disease resistance (Pietsch et al., 2020).

8 Case Study: Environmental Stress-Driven Disease Outbreaks in Intensive Turbot Farming Systems

8.1 Overview of typical industrial recirculating aquaculture systems (RAS) and net pen systems

Industrial turbot farming is increasingly centered on land-based recirculating aquaculture systems because they permit intensive production under controlled indoor conditions and reduce exposure to external climatic variability. In turbot RAS, production water typically passes through linked compartments that include fish tanks, sedimentation units, biofilters, and ozone or protein-skimming chambers, allowing continuous control of temperature, dissolved oxygen, salinity, and nitrogenous wastes (Ahmed and Turchini, 2021). This engineering design supports high stocking density and stable production, which is one reason RAS has become widely used in turbot culture.

However, the same water-saving and high-density features that make RAS efficient can also concentrate biological and chemical risks when management is suboptimal. Reduced water exchange can permit the accumulation of growth-inhibiting factors, bacterial metabolites, and dissolved contaminants, while treatment performance may become unstable across season, hydraulic regime, and biomass load. Net pen systems differ in that they rely on natural water exchange rather than closed-loop treatment, so they generally experience greater direct exposure to fluctuations in temperature, oxygen, and other environmental drivers that can precipitate stress-linked disease events (Ahmed and Turchini, 2021).

8.2 Multi-factorial stress interaction (temperature-oxygen-ammonia coupling effects)

Disease risk in intensive turbot farming is rarely driven by a single variable, because temperature, oxygen, and ammonia interact at both physiological and production levels. Elevated temperature is a major stressor in this cold-water species and has been linked with rapidly increasing disease-induced mortality above 20°C, while high ammonia exposure activates the hypothalamic-pituitary-interrenal axis and suppresses humoral immune indicators such as lysozyme, complement, and IgM. This means that warming and ammonia accumulation can jointly weaken host resistance even before a specific pathogen is identified.

Oxygen availability modifies the severity of ammonia toxicity and therefore changes outbreak risk under intensive culture. In juvenile turbot, chronic un-ionised ammonia above 0.17 mg L^-1 reduced growth under normoxic conditions, whereas hyperoxia increased tolerance to ammonia, indicating that oxygen management can partly buffer toxic nitrogen stress (Gao et al., 2023). Evidence from another marine fish model points in the same direction mechanistically: ammonia exposure under higher temperature increased cortisol and *hsp70*, disrupted antioxidant balance, and reduced innate immune functions, supporting the view that coupled thermal and nitrogen stress can intensify physiological collapse in aquaculture systems.

8.3 Disease outbreak case analysis and management implications

Field and farm observations show that bacterial disease outbreaks remain the dominant health problem in intensive turbot production. A three-year epidemiological survey in China found that bacteria were isolated from 137 of 155 investigated disease cases, with Edwardsiella piscicida and *Aeromonas salmonicida* together accounting for about 71% of all cases, demonstrating that stress-sensitive bacterial pathogens dominate real farm losses (Gao et al., 2023). A separate RAS study detected potential pathogens such as Photobacterium damselae, Tenacibaculum discolor, Tenacibaculum soleae, and Serratia marcescens throughout multiple system compartments even in the absence of overt disease, indicating that intensive systems can harbor persistent background pathogen pressure.

Management implications therefore center on preventing environmental deterioration before it converts latent pathogen presence into clinical outbreak. During an Edwardsiella outbreak in turbot RAS, higher ozone treatment improved survival and reduced heterotrophic bacteria, *Vibrio* loading, and nitrite relative to lower-control conditions, suggesting that tighter water-quality control can reduce outbreak severity even when it does not fully remove infection pressure. At the population level, the marked decline in E. piscicida case proportion after vaccine introduction further indicates that outbreak control is strongest when environmental management is combined with targeted prophylaxis rather than relying on antibiotics alone, especially given the reported increase in antibiotic resistance over time (Gao et al., 2023).

9 Integrated Management Strategies for Health Improvement

Environmental monitoring and early warning systems are increasingly central to health management in turbot farming because intensive aquaculture depends on detecting water-quality instability before it causes physiological stress or mortality. In recirculating aquaculture systems, real-time monitoring of basic parameters such as dissolved oxygen, pH, temperature, turbidity, and salinity is already technically feasible, and IoT-based systems combined with artificial intelligence can generate warnings when conditions approach critical thresholds. This is especially important in turbot culture because emerging evidence shows that dissolved wastes such as phosphate can cause gill, liver, and spleen injury at high concentrations, reinforcing the need to expand monitoring beyond only traditional variables.

Early warning capacity is strengthened when environmental sensing is paired with anomaly detection, behavioral observation, and predictive analytics rather than relying on periodic manual measurements alone. Aquaculture monitoring platforms now support continuous data transmission, automated warning scores, and real-time visualization, while AI-based systems can detect deviations in fish behavior and water quality patterns quickly enough to support preventive intervention. In parallel, biosensor frameworks and biological early warning systems indicate that physiological or organism-level responses can provide a real-time signal of pollution or other stressors before overt disease develops, which is highly relevant for intensive turbot production under fluctuating environmental loads.

Water quality regulation in turbot systems should focus on preventing the accumulation of nitrogenous wastes, phosphate, and other dissolved metabolites while stabilizing hydraulic and feeding conditions that support biofilter function. In turbot RAS, treatment performance can vary with season, biomass, and recycle rate, and earlier farm-scale work showed instability in solids and nutrient removal under changing outdoor conditions, indicating that regulation must be adaptive rather than static. More recent turbot evidence also shows that feeding frequency affects ammonia and nitrite dynamics, with feeding twice daily producing the highest removal rates and the most stable water environment, likely because this regime better matches digestion and supports nitrification-linked microbial functions.

Biofiltration optimization should therefore integrate engineering control with husbandry management, because microbial treatment efficiency depends on both reactor design and the waste-loading pattern imposed by farming practice. General RAS evidence shows that recirculation can reduce ammonia by more than 80% and phosphate by more than 70%, but persistent high-ammonia zones can still emerge where aeration or local operation is suboptimal. For turbot specifically, continuous phosphate surveillance is now justified because juveniles tolerated 60 mg/L through compensatory tissue repair responses, whereas 120 mg/L caused apoptosis in gill tissue and broader hepatic and immune injury, meaning that dissolved nutrient control should target prevention of chronic sublethal toxicity as well as acute failure.

Probiotic and immunostimulant strategies offer a practical complement to environmental control by strengthening host resilience against the background pathogen pressure typical of intensive turbot farming. In juvenile turbot, dietary oregano oil and Bacillus coagulans improved growth, digestive capacity, and resistance to *Aeromonas salmonicida*, while host-associated Bacillus velezensis T20 improved intestinal antioxidant capacity, barrier function, microbiota composition, and survival after *Edwardsiella tarda* challenge. Native or host-adapted microbial candidates appear especially promising because prophylaxis is more effective than reactive treatment in early life stages, and beneficial strains can reduce mortality without depending on antibiotic-based control.

Adaptive farming strategies should combine these functional feeds with environmental adjustment of flow, hygiene, and routine operations to reduce chronic stress exposure. In turbot RAS, a flow velocity around 0.9 body lengths per second promoted feed intake, growth, and innate immune indicators, whereas higher velocity acted as a stressor and reduced growth, showing that hydrodynamic settings are a manageable component of health support. Newer dietary interventions also broaden the toolkit: multi-strain probiotics improved enzyme activity and intestinal structure, B. coagulans helped restore microbial homeostasis after antibiotics, and postbiotics from Cetobacterium somerae improved gut health and disease resistance, supporting a shift toward integrated, low-antibiotic health management in turbot aquaculture.

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Effects of Different Farming Systems on Growth Performance and Survival of Chinese Sea Bass (*Lateolabrax maculatus*)

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Abstract As an important commercial marine fish species for aquaculture in my country, the growth performance and survival rate of the spotted sea bass (*Lateolabrax maculatus*) depend heavily on the type of culture system and its capacity for environmental control. This paper reviews and compares the mechanisms by which pond culture, net-pen culture, and recirculating aquaculture systems (RAS) influence growth performance and survival rates. The results indicate significant differences among these systems regarding water quality stability, dissolved oxygen supply, ammonia-nitrogen accumulation, and stocking density management, leading to variations in growth rates and feed conversion ratios (FCR). Among them, RAS typically demonstrates superior growth efficiency and lower mortality due to robust water quality control and stable environmental conditions; pond systems are significantly affected by natural environmental fluctuations, resulting in less stable growth and survival; net-pen systems fall between the two but are susceptible to the effects of water exchange and seasonal changes. Comparative analysis further reveals that environmental stability and nutrient utilization efficiency are key determinants of aquaculture performance. Additionally, the incidence of disease and stress responses intensifies under high-density culture conditions. Based on this comparative analysis, the paper proposes optimized culture models and environmental management strategies to enhance the sustainability and productivity of spotted sea bass aquaculture.

Keywords Spotted sea bass; Culture system; Recirculating aquaculture system (RAS); Growth performance; Survival rate

1 Introduction

Chinese sea bass (*Lateolabrax maculatus*) has become an increasingly important aquaculture species in China over the past two decades, with the industry expanding rapidly and contributing substantially to the national fishery economy (Huang et al., 2025). This development is closely linked to the species' favorable biological characteristics, especially its rapid growth rate and strong adaptability to a range of environmental conditions, which have supported its broad culture potential and increasing industrial relevance. At the same time, progress in Chinese sea bass aquaculture has depended on advances across multiple fields, including breeding, seed production, nutrition, and disease management, indicating that further gains in production will likely require continued integration of biological and farming technologies. Despite these achievements, the industry still faces important constraints, including low profitability and insufficient risk management relative to other major farmed fish sectors, which highlights the need for research that can support higher-quality and more efficient development.

Among the major factors shaping aquaculture productivity, the choice and optimization of farming system is especially important because production environment directly influences fish growth, health status, resource use, and overall economic return (Li et al., 2023). Comparative work on Chinese sea perch culture systems has shown clear differences in ecological-economic performance among pond farming, offshore cage culture, and cage culture, with offshore cage culture identified as the most sustainable among the current main marine fish farming systems in China (Zhang et al., 2021). More broadly, research on modern recirculating aquaculture systems indicates that controlled land-based production can reduce water use, improve water quality, lower disease risk, and strengthen waste management, all of which are directly relevant to improving production efficiency and survival in intensive fish culture (Gupta et al., 2024). These findings suggest that farming-system design is not only a management issue but a central biological and economic determinant of aquaculture performance.

Evidence from other cultured fish further supports the view that system optimization can markedly alter growth and survival-related outcomes. In grass carp, the recirculating pond aquaculture system produced lower concentrations of ammonia, nitrite, and nitrate nitrogen than traditional ponds, while also improving growth rate and feed conversion, indicating that better environmental control can translate into more efficient production (Xu et al., 2025). In largemouth bass, a funnel-shaped recirculating aquaculture system generated significantly higher body weight and stronger antioxidant capacity than a traditional pond system, suggesting that improved hydrodynamics and water treatment can enhance both growth and physiological condition (Xu et al., 2025). Similar trends have also been reported in hybrid grouper, where fish reared in a recirculating aquaculture system showed better growth performance and lower *Vibrio* concentrations in tissues than fish in a simulated pond system, linking farming mode to both productivity and health protection. Although these studies involve species other than Chinese sea bass, they provide a strong comparative basis for expecting measurable effects of farming systems on growth performance and survival.

Against this background, evaluating the effects of different farming systems on Chinese sea bass is both scientifically necessary and practically valuable. Chinese sea bass aquaculture has advanced substantially, but the lack of integrated system-level assessment remains a barrier to the industry's high-quality development and to clearer identification of future goals (Huang et al., 2025). Experimental evidence in spotted sea bass already shows that environmental conditions characteristic of different systems, such as flow velocity, can shift growth, lipid metabolism, and oxidative stress responses, demonstrating that production settings can create biological trade-offs rather than simple uniform benefits (Li et al., 2023). Therefore, the present study aims to compare different farming systems for L. *maculatus* by focusing on growth performance and survival, with the broader goal of clarifying which culture conditions are more favorable for efficient and sustainable production. The scope of this study is to provide an evidence-based basis for farming system optimization in Chinese sea bass aquaculture and to contribute to the ongoing transition of the industry toward greater productivity, resilience, and environmental compatibility.

2 Biological Characteristics and Growth Requirements of *Lateolabrax maculatus*

2.1 Growth performance and feeding behavior characteristics

Lateolabrax maculatus is widely regarded as a promising aquaculture species because it combines rapid growth with broad farming applicability across marine and low-salinity systems (Huang et al., 2025). Growth performance in this species is strongly shaped by nutritional composition, especially dietary protein and lipid balance. Under controlled feeding trials, juveniles reared at 27 °C achieved their highest weight gain when diets contained about 47% crude protein, and feed conversion improved as protein level increased up to that point. Growth is also sensitive to dietary energy partitioning, because optimal protein-to-energy ratios differed with temperature, indicating that efficient tissue deposition depends on both feed formulation and the rearing environment rather than nutrient level alone (Lu et al., 2020).

Feeding behavior in Chinese sea bass shows a clear link to growth efficiency. Juveniles fed to apparent satiation two or three times daily displayed higher weight gain, specific growth rate, feed efficiency, and protein efficiency ratio than fish fed less frequently, while performance was not meaningfully improved beyond twice-daily feeding. Feed quality further modifies this response. Diets with an n-3/n-6 polyunsaturated fatty acid ratio near 0.66 produced the highest final body weight, weight gain, specific growth rate, and protein efficiency ratio, together with the lowest feed conversion ratio (Dong et al., 2023). Recent neuroendocrine evidence also indicates that feeding and growth are physiologically integrated, with temperature- and salinity-responsive stress pathways activating anorexigenic and growth-inhibitory signals that ultimately suppress intake and growth under unfavorable conditions (Li et al., 2023).

2.2 Environmental adaptability and stress response

Chinese sea bass is a euryhaline species with unusually broad salinity tolerance, which explains its suitability for culture in seawater cages, brackish environments, and freshwater ponds (Zhu et al., 2023). Available evidence indicates that the species can survive from freshwater to high-salinity seawater conditions, although growth is not

equally supported across that entire range. Earlier work identified an optimal salinity around 16-17 ppt, and long-term acclimation experiments showed that growth remained stable at 0, 12, and 30 ppt but was significantly inhibited at 45 ppt (Li et al., 2023). Salinity challenge therefore demonstrates both strong environmental plasticity and a measurable cost when osmotic demand becomes excessive.

The stress response of L. *maculatus* is similarly environment-dependent. Moderate salinity elevation to 24 psu appears to improve protein utilization, whereas salinity stress also alters Na+/K+-ATPase activity, oxidative damage markers, and the expression of genes involved in energy metabolism, immunity, and osmoregulation (Hu et al., 2024). Temperature is another major regulator. Growth after 30 days was 2.76-3.22 times better at 21 °C than at 14 °C or 28 °C, showing that both low and high temperature can constrain performance even in an adaptable species (Li et al., 2023). At the molecular level, environmental stress activates coordinated defense pathways, including heat shock protein responses under thermal challenge and broad gill transcriptomic remodeling under salinity or alkalinity stress, confirming that adaptability depends on active cellular compensation rather than passive tolerance alone (Zhu et al., 2023).

2.3 Physiological constraints on survival and development

Despite its adaptability, Chinese sea bass faces clear physiological constraints that limit survival and normal development under chronic or acute stress. Early life stages occur in estuarine nursery habitats where temperature and salinity fall within relatively defined ranges, indicating that successful larval development depends on suitable brackish-water conditions rather than unrestricted environmental tolerance. In juveniles, thermal stress sharply increases vulnerability. Larger juveniles experience higher oxidative stress, more severe liver damage, and greater mortality than smaller individuals under acute heat exposure, suggesting that body size influences thermal resilience during culture (Qin et al., 2023). These findings show that survival is shaped not only by the external environment but also by ontogenetic stage and internal physiological capacity.

Long-term heat exposure imposes even broader constraints on organ function and whole-animal survival. At 35 °C, juvenile Chinese sea bass showed increased mortality together with oxidative damage, inflammation, apoptosis, and strong induction of heat shock proteins, indicating that compensatory defenses are activated but are insufficient to fully prevent injury (Yang et al., 2025). Prolonged high temperature also caused gill remodeling, liver vacuolization, reduced and broken intestinal villi, depressed digestive enzyme activities, and weakened nonspecific immune capacity, which together reduce oxygen uptake, digestion, tissue repair, and disease resistance. Survival can also decline rapidly during handling-related stress: during 9 h of simulated waterless transport, survival dropped markedly and major biochemical disturbances developed, indicating that confinement and impaired homeostasis are important non-growth constraints in production chains (He et al., 2020).

3 Overview of Different Farming Systems

3.1 Pond culture systems

Pond culture is one of the principal farming modes used for *Lateolabrax maculatus* in China, and it remains especially representative in the Bai Jiao production area of Guangdong because local hydrological conditions favor this model (Huang et al., 2025). In practice, pond systems are semi-enclosed and usually depend on tidal exchange, which makes them relatively easy to manage because of their smaller water volume, but also ties production performance closely to surrounding water conditions (Zhang et al., 2021). This basic structure supports both extensive and semi-intensive production. Extensive ponds rely more on natural productivity and lower external inputs, whereas semi-intensive ponds use greater feed input, higher stocking densities, and more active water management to raise output while still retaining the operational simplicity of earthen or coastal pond infrastructure.

The main strengths of pond systems are flexibility and comparatively straightforward husbandry, but their biological performance depends strongly on density control and water quality stability. In intensively managed earthen ponds for seabass, survival did not differ significantly among tested stocking densities, yet fish stocked at 6 fish/m^2 achieved significantly greater final weight and daily weight gain than those stocked at 10 fish/m^2 (Nhan et al., 2022). Pond environments also influence fish health through their microbial conditions, because sea bass ponds with high

mass mortality showed bacterial community structure and function that differed significantly from low-mortality ponds (Deng et al., 2021). These findings indicate that pond farming can support strong production, but as semi-intensive management increases, growth and survival become more sensitive to ecological imbalance, crowding, and deterioration of the pond environment.

3.2 Cage and net pen aquaculture systems

Cage and net pen aquaculture is the other major farming system for Chinese sea bass, and it is widely used in sheltered marine waters where open-water exchange can support intensive fish production (Zhang et al., 2021). In these systems, fish are confined within mesh enclosures while surrounding water flows freely through the cage, which facilitates feeding, observation, and harvesting while also helping to maintain water quality and disperse wastes. This makes cage farming attractive for carnivorous, high-value fish such as sea bass. However, the same openness that improves exchange also exposes stocks and infrastructure to waves, currents, temperature shifts, and other external stressors, so site selection and engineering design are central to production success.

Performance in cage culture depends heavily on stocking density, hydrodynamics, and structural stability. In open-sea floating net cages, *Asian seabass* stocked at 10 fish/m^3 showed the best overall growth and production metrics, indicating that moderate density can outperform both lower and higher loading under offshore conditions (Figure 1) (Mostofa et al., 2024). At the same time, cage systems are mechanically sensitive because nets bear most hydrodynamic load, can deform under waves and currents, and thereby reduce culture space and water exchange, both of which affect fish welfare. Environmental modeling for deep-sea sea bass cages in the Yellow Sea further suggests that water-column quality can remain acceptable, although organic wastes may still accumulate in underlying sediments, highlighting the need for careful layout and environmental monitoring in offshore expansion.

3.3 Recirculating aquaculture systems and industrialized systems

Recirculating aquaculture systems (RAS) and other industrialized land-based systems represent a more controlled farming strategy in which water is repeatedly reused after mechanical and biological treatment (Lindholm-Lehto, 2023). These systems are increasingly promoted because they reduce water consumption and environmental discharge while allowing farmers to regulate key production variables more precisely than in ponds or sea cages (Li et al., 2023). As a result, RAS and industrialized systems are particularly relevant where biosecurity, standardized production, and year-round environmental control are priorities. Their technological basis also aligns with the broader trend toward more intensive and mechanized aquaculture development in China and elsewhere.

The main advantage of RAS is continuous environmental control, but this benefit depends on effective treatment and monitoring because wastes can accumulate rapidly in closed-loop systems. Hazardous substances such as particulate matter, ammonia, nitrite, and nitrate can build up from feeding and excretion and directly threaten fish safety and system operation if treatment performance declines (Li et al., 2023). Evidence from integrated land-based recirculating production shows that water-quality variation within the system is reflected in final weight, survival, specific growth rate, and yield, confirming that fish production responds directly to the success of recirculation management. Modern RAS therefore offers strong potential for improving growth consistency and survival of Chinese sea bass, but its practical value depends on reliable biofiltration, oxygenation, and real-time monitoring rather than on water reuse alone.

4 Effects of Farming Systems on Growth Performance

4.1 Growth rate differences across culture systems

Growth performance differs across culture systems because ponds, cages, and recirculating systems expose fish to distinct combinations of flow, salinity, density, and environmental stability. In Chinese sea bass, pond aquaculture and marine net-cage aquaculture remain the two dominant production modes, and recent industry review evidence notes that desalinated fish in pond-based production can grow about one-third faster than those reared in seawater, although high-density freshwater pond farming can reduce product quality (Huang et al., 2025). At the same time, offshore cage culture appears more favorable than conventional cage culture in ecological-economic performance, suggesting that differences among open-water systems are also biologically and operationally meaningful rather

than merely structural (Zhang et al., 2021). System-specific hydraulic conditions further help explain these differences. Experimental work designed to mimic land-based RAS and deep-sea cage flow regimes showed that higher flow velocities enhanced growth performance relative to low-flow conditions in L. *maculatus*, while a separate velocity trial found the best specific growth rate and weight gain at a moderate flow of 1.14-1.56 body lengths/s rather than at still water or the highest velocity (Fei et al., 2025).

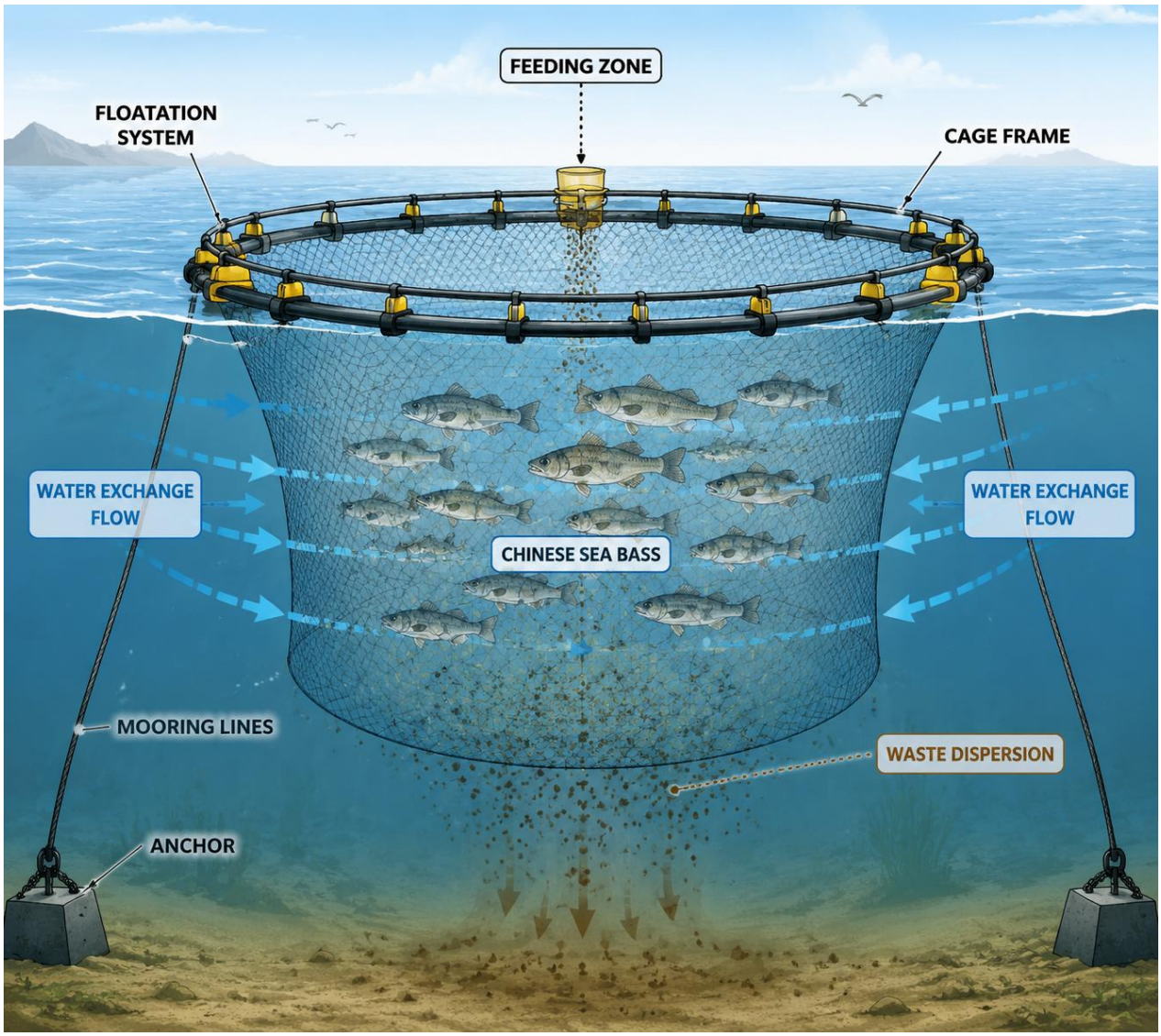

Figure 1 Schematic representation of a marine cage and net pen aquaculture system used for Chinese sea bass culture

Evidence from other cultured bass supports the same pattern: systems that provide more stable and better-controlled rearing conditions often produce faster growth, but only within appropriate density and engineering limits. In largemouth bass, a funnel-shaped recirculating system produced significantly higher body weight than a traditional pond system, indicating that industrialized water treatment and circulation can improve growth outcomes over conventional pond culture (Xu et al., 2025). In European sea bass net pens, growth rate increased linearly with cage volume, reaching 0.68 g/day in large cages versus 0.56 and 0.32 g/day in medium and small cages, respectively, showing that even within cage farming, physical scale can materially affect growth. Recirculating systems also have density thresholds. In tank-based RAS for sea bass, daily feed intake and specific growth rate were maintained up to 70 kg/m^3, but growth declined above that level, with specific growth rate about 14% lower at 100 kg/m^3. Taken together, the evidence indicates that no farming system guarantees superior growth on its own; performance depends on how well each system controls the specific environmental factors that constrain growth.

4.2 Feed conversion efficiency and nutrient utilization

Feed conversion efficiency is a central indicator of farming performance, but it should be interpreted together with broader nutrient-use metrics. In aquaculture, FCR is defined as feed administered divided by weight gained, and it remains the most widely used measure of production efficiency. However, FCR alone does not capture feed composition, edible yield, or nutrient quality of harvested fish, so nutrient retention offers an important complementary perspective when comparing farming systems or feeds. For Chinese sea bass, diet-quality studies show that feed utilization is highly responsive to nutritional balance. A dietary n-3/n-6 PUFA ratio of 0.66 produced the highest final body weight, weight gain, specific growth rate, and protein efficiency ratio, together with the lowest FCR, indicating that system performance depends partly on whether the culture environment allows efficient use of a biologically appropriate diet (Dong et al., 2023). Thus, comparisons among farming systems should consider not only how much feed is consumed, but how effectively environmental conditions translate that feed into growth and retained nutrients.

System conditions can improve or impair feed utilization by altering oxygen availability, crowding, digestion, and activity level. A broad endocrine review shows that low dissolved oxygen reduces growth, feed intake, and overall fish performance, and that FCR is inversely related to dissolved oxygen, making water-quality control a direct determinant of feed efficiency (Canosa and Bertucci, 2023). Density has similar effects. In *Amur sturgeon*, increasing stocking density reduced feeding rate and increased FCR, and the growth suppression was linked to lower food intake and poorer food conversion efficiency under crowding stress. In *Asian seabass* reared in RAS, higher stocking density significantly decreased both growth performance and feed utilization efficiency, while lower-density fish also maintained higher digestive enzyme activities and protein deposition (Ezhilmathi et al., 2022). By contrast, moderate hydrodynamic stimulation can support nutrient use: in Chinese sea bass, moderate flow increased digestive enzyme activity and improved growth, while in simplified indoor recirculating systems, continuous water flow appears to enhance exercise-related protein deposition in muscle. These results suggest that farming systems improve FCR and nutrient utilization when they minimize physiological stress while maintaining water movement, oxygenation, and feeding conditions within the species' optimum range.

4.3 System-related growth regulation mechanisms

The effects of farming systems on growth are mediated by physiological regulation rather than by environment alone. Fish growth is controlled primarily through the GH/IGF axis, and this axis is strongly influenced by external factors such as temperature, salinity, photoperiod, pollutants, and stocking density. More generally, fish performance reflects an interaction between genetic potential and immediate environmental conditions, and adverse conditions such as poor water quality, disturbance, or social stress reduce growth through endocrine pathways rather than through simple feed limitation alone. In Chinese sea bass specifically, temperature and salinity changes regulate growth through a stress-feeding-growth neuroendocrine cascade. Growth after 30 days was markedly better at 21 °C than at 14 °C or 28 °C, and transcriptomic analysis identified responsive modules linking stress signaling to feeding and growth control. This means that farming systems differ in growth outcome partly because they differ in how strongly they activate or suppress these endocrine networks.

Several mechanisms identified across the evidence base are directly relevant to system design. In L. *maculatus*, stress-induced heat shock proteins appear to activate the hypothalamic-pituitary-interrenal axis, then stimulate anorexigenic genes and growth-inhibiting somatostatin, providing a plausible pathway by which unfavorable thermal or salinity conditions suppress feeding and growth. Hydrodynamic conditions also regulate metabolism at the molecular level: higher flow enhanced growth but increased oxidative stress, and transcriptomic analysis identified *foxo3* and the FoxO signaling pathway as key hubs coordinating oxidative stress mitigation and energy mobilization. Density-related regulation follows a similar pattern. In juvenile Chinese sturgeon reared in RAS, high density elevated ACTH, cortisol, glucose, lactate, and HSP70 while down-regulating GH and IGF-I, whereas in *Asian seabass* increasing density down-regulated the GH/IGF axis and up-regulated myostatin. At the tissue-growth level, muscle development depends on GH, IGFs, TOR-related signaling, and myogenic regulators, so any farming system that chronically disrupts endocrine balance, oxygen supply, or activity pattern is likely to limit growth even when feed is abundant.

5 Survival Rate and Mortality Patterns under Different Systems

5.1 Disease incidence and mortality dynamics

Disease is a major source of mortality in sea bass culture, and outbreaks can cause rapid stock losses when pathogen exposure coincides with intensive farming conditions (Yue and Guo, 2025). In Chinese sea bass specifically, pond investigations in Zhuhai found clear contrasts between high- and low-mortality ponds, with the high-mortality pond showing significantly different bacterial community structure and function, indicating that mortality events are closely tied to the surrounding microbial environment (Deng et al., 2021). This pattern suggests that disease incidence in pond systems is not only a matter of host infection, but also of ecological imbalance in the culture water. As pond systems become more intensified, the probability that unfavorable microbial shifts will amplify mortality risk appears to increase.

Pathogen-specific studies show that mortality dynamics can be abrupt and severe in both pond and cage systems. In farmed L. *maculatus*, *Aeromonas veronii* caused acute death marked by hemorrhagic lesions, and experimental infection produced mortality within 24 h, reaching 100% at the highest challenge dose (Wang et al., 2022). In marine cage culture, a sudden disease outbreak with significant mortality was linked to coinfection by *Vibrio harveyi* and *Photobacterium damselae* subsp. *piscicida*, and dual infection produced faster and more pronounced mortality than single-pathogen challenge (Zhou et al., 2024). Together, these findings indicate that mortality under different farming systems depends not only on whether pathogens are present, but also on whether the system promotes pathogen proliferation, coinfection, and rapid transmission through dense fish populations.

5.2 Environmental stability and survival regulation

Environmental stability is a direct regulator of survival because fish mortality rises when water quality fluctuates beyond the range that the stock can physiologically tolerate. In earthen pond seabass culture, survival remained statistically similar across the tested densities when temperature, dissolved oxygen, pH, salinity, transparency, and ammonia stayed within suitable ranges, showing that stable water conditions can buffer survival even when density increases (Nhan et al., 2022). More broadly, seabass culture reviews identify site suitability, salinity maintenance, and water quality control as basic requirements for reducing mortality in both pond and cage farming. This means that system effects on survival are mediated less by the label of the system itself than by how consistently that system maintains acceptable culture conditions.

Recirculating and industrialized systems aim to improve survival precisely by stabilizing the rearing environment. Good water quality in RAS is described as crucial for successful growth and survival, and real-time monitoring is increasingly used to provide warnings of critical situations before they develop into mortality events (Lindholm-Lehto, 2023). Evidence from seabass culture also indicates that inconsistent water quality and traditional tank management can lead to contaminant accumulation, disease, stunted growth, and high mortality, whereas RAS-based white seabass culture achieved survival above 75% under maintained water quality conditions (Jais et al., 2024). These results support the view that environmental regulation is one of the main survival advantages of recirculating systems, although that advantage depends on reliable filtration, sensor performance, and timely management responses.

5.3 Stress-induced mortality mechanisms

Stress-induced mortality typically develops through chronic crowding, endocrine activation, oxidative damage, and immune suppression rather than through a single isolated event. High stocking density in cultured fish consistently elevates cortisol and other stress indicators, and in juvenile Chinese sturgeon reared in RAS it also suppressed growth and reduced immune and antioxidant capacity. Comparable evidence from grass carp shows that long-term overcrowding increases cortisol, decreases lysozyme, complement, and IgM, and drives an unbalanced inflammatory response, demonstrating a plausible mechanistic path from crowding stress to greater vulnerability and eventual mortality (Li et al., 2023). These mechanisms are highly relevant to Chinese sea bass because farming systems differ fundamentally in crowding intensity, water exchange, and the persistence of stress exposure.

Stress can also alter survival indirectly by weakening the fish before pathogen or environmental insults occur. In striped catfish, increasing stocking density elevated un-ionized ammonia and nitrite while lowering dissolved oxygen, and survival decreased significantly as density increased, linking environmental deterioration to physiological stress and mortality (Zaki et al., 2023). In marine fish more broadly, high stocking density produces chronic stress, raises plasma cortisol about fourfold, and depresses immune function, which helps explain why intensive systems can show mortality even when outright disease is not initially apparent. For L. *maculatus*, stress-induced mortality under different farming systems therefore appears to arise from the interaction of crowding, reduced water quality, impaired immunity, and increased susceptibility to opportunistic infection.

6 Water Quality and Environmental Regulation Effects

6.1 Dissolved oxygen, ammonia, and nitrogen accumulation

Dissolved oxygen and nitrogenous waste are among the main environmental constraints separating pond, cage, and recirculating systems. Across aquaculture systems, production is progressively limited by oxygen supply and the accumulation of growth-limiting wastes such as ammonia, while in RAS the removal of nitrogen pollutants remains difficult because wastewater typically has high dissolved oxygen but low organic carbon for denitrification (Ott et al., 2025). This matters directly for Chinese sea bass because high-density holding already shows the expected deterioration pattern: during simulated live transport, higher density reduced dissolved oxygen and increased total ammonia nitrogen, indicating how quickly confined systems can shift toward stressful water chemistry (Zhang et al., 2021). In pond systems, the pattern is somewhat different because natural biogeochemical processes buffer part of the ammonia load, but that buffering weakens as feed input and aeration intensity rise.

System design determines whether added nitrogen accumulates as toxic reduced forms or is pushed into less harmful oxidized forms. In intensively aerated earthen ponds, average total ammonia and un-ionized ammonia did not increase with higher stocking density, while nitrite and nitrate increased, indicating that nitrification became a more important ammonia-removal pathway under high loading. Similarly, ponds managed at a higher minimum dissolved oxygen concentration produced fish that were 35% larger, and the higher-oxygen treatment also had higher nitrite and nitrate, consistent with greater oxidation of ammonia through nitrification (Ott et al., 2025). In RAS, oxygen management can also directly suppress reduced nitrogen compounds: microbubble aeration stabilized dissolved oxygen at 4.28 mg/L and reduced both carbon dioxide and ammonia, while optimized MBBR operation reached 50% TAN removal once dissolved oxygen conditions supported biofilm performance.

6.2 Temperature fluctuation and seasonal variability

Temperature fluctuation affects farming systems not only through direct fish physiology but also by altering the stability of the rearing environment. Across aquaculture species, temperature is a major abiotic driver of growth and survival, and temperatures above species-specific thermal thresholds reduce performance, health, and productivity (Mugwanya et al., 2022). Extreme temperature events are also becoming more frequent and more intense, and they influence metabolism, immunity, and stress responses across cultured fish, which means that systems with poor thermal buffering are more exposed to seasonal production losses. For Chinese sea bass, this issue is especially relevant because open ponds and cages are more directly affected by ambient seasonal variation than industrialized land-based systems.

Evidence from Chinese sea bass and other farmed fish suggests that both average temperature and short-term fluctuation matter. During temporary holding and transport, L. *maculatus* was maintained at 20 °C-22 °C before cooling to 12 °C, illustrating that temperature is actively controlled to reduce stress in intensive handling conditions rather than left to fluctuate freely (Zhang et al., 2021). More broadly, daily fluctuation between 27 °C and 18 °C in Nile tilapia suppressed immune function, elevated heat-shock responses, and increased mortality after bacterial challenge to 35%-40%, showing how unstable temperature can worsen disease vulnerability even when mean conditions appear acceptable. Seasonal water instability can interact with nitrogen dynamics as well: in an aquaponics comparison, the control system experienced sharp ammonia accumulation followed by a nitrite spike to 13 mg/L, and all fish died, whereas the regulated system maintained more stable water quality and avoided those losses (Huang et al., 2025).

6.3 Biofiltration capacity and self-purification differences

Biofiltration capacity is one of the clearest differences among farming systems. In RAS, nitrogenous wastes cannot be controlled safely without in situ nitrification and denitrification through biofilters or bioreactors, and different systems support distinct nitrifying communities that determine how effectively nitrogen is converted and removed. By contrast, ponds depend more heavily on natural self-purification in the water column and sediment interface, which makes them biologically flexible but less predictable under high feeding and organic loading (Ott et al., 2025). This distinction is central to Chinese sea bass farming because more industrialized systems replace ecological buffering with engineered microbial treatment, while traditional ponds rely more on sediment processes, phytoplankton uptake, and water exchange.

Recent work shows that engineered biological treatment can substantially improve both water quality and production, but outcomes depend on the treatment pathway used. In recirculating ponds, adding a bacteria-microalgae association with biofilm carriers reduced TN by 29.15%, TAN by 51.28%, and nitrite-N by 33.48%, while fish production increased by 13.3% (Wang et al., 2022). Advanced oxidation in RAS similarly reduced NH_4^+-N and NO_2^--N, and O_3/UV treatment also increased fish length and weight, although it increased antibiotic resistance genes and therefore introduced a clear biosafety trade-off (Xue et al., 2023). Other side-loop treatments show comparable promise: woodchip denitrification with sand filtration achieved 96% denitrification efficiency and supported safe water reuse, while nitrate diffusion from RAS tailwater into pond sediments improved native sediment denitrification and lowered sediment ammonium accumulation (Lindholm-Lehto et al., 2021; Jia et al., 2022).

7 Feeding Management and Behavioral Adaptation

7.1 Feeding frequency and feeding strategy differences

Feeding frequency is a major determinant of growth efficiency in sea bass culture because it governs feed access, digestive loading, and the regularity of nutrient supply. In *Asian seabass* fry, feeding three times daily produced the best final body weight, specific growth rate, feed conversion, and survival, whereas feeding once daily gave the poorest overall performance (Hassan et al., 2021). A second fingerling study reached the same practical conclusion, showing that feeding frequency significantly affected feed intake, feed utilization efficiency, protein efficiency ratio, and relative growth rate, with the best results again at three meals per day. For Chinese sea bass production, this supports the use of moderate meal frequency as a core management tool, especially in systems where fish competition and feed loss are likely to increase under low-frequency feeding schedules.

Feeding strategy interacts with the farming environment rather than operating as a fixed rule across systems. In a freshwater aquaponic system for sea bass, four or eight meals daily produced higher final weight, weight gain, and specific growth rate than two meals, while survival was not affected by feeding frequency itself. By contrast, striped bass reared in recirculating systems showed no growth or efficiency penalty when feeding frequency was reduced, because fish compensated by eating more per meal and less over the full trial. These results indicate that optimal feeding schedules for L. *maculatus* are likely to depend on whether the system is a pond, cage, aquaponic, or RAS environment, since water exchange, feed recovery, and fish access to pellets differ substantially among those systems.

7.2 Behavioral adaptation under different farming environments

Behavioral adaptation to farming conditions is strongly shaped by density, oxygen availability, and the predictability of feeding. Under high stocking density, farmed fish often shift toward more cohesive and synchronized group behavior, and in gilthead sea bream this included reinforced schooling and a more clearly organized swimming rhythm centered on feeding time. High-density fish also showed reduced feed intake and growth, indicating that behavioral coordination under crowding is adaptive for coexistence but not necessarily favorable for production (Holhorea et al., 2023). For Chinese sea bass, similar adjustments are likely in cage and intensive pond systems, where crowding and competitive feeding can force fish to prioritize synchronized access to feed over low-cost routine behavior.

Feeding method also alters social behavior and risk responses. In juvenile seabream, hand-feeding improved body weight relative to self-demand feeding, while self-demand systems appeared to reinforce social hierarchy and competitiveness for resources within the group. Behavioral responses to rearing conditions are also density dependent but not always linear, because zebrafish held at the lowest density showed more aggression and higher cortisol than fish at intermediate or high density, even though high-density fish had lower and more variable growth rates (Sarma et al., 2023). This suggests that behavioral adaptation in aquaculture involves balancing social stress at both extremes: overly sparse groups can destabilize social interactions, whereas overly crowded groups can suppress feeding performance and increase competition, making intermediate density and predictable feeding especially important for sea bass welfare.

7.3 Nutritional physiology and energy allocation trade-offs

Nutritional physiology in farmed fish reflects a trade-off between growth, maintenance, and the metabolic capacity to cope with environmental challenge. Longitudinal data across teleosts show that faster ontogenetic growth is positively associated with standard metabolic scaling but negatively associated with aerobic scope, indicating that accelerated growth can reduce the metabolic margin available for functions beyond maintenance. A broader ecophysiological analysis in salmonids identified a similar dominant trade-off between high growth and consumption on one side and high aerobic scope and active metabolism on the other. In farming terms, systems that maximize growth through high ration and frequent feeding may therefore also narrow the physiological buffer available for activity, hypoxia tolerance, or other stress responses.

These trade-offs become more visible under intensive farming conditions that alter oxygen demand and energy partitioning. In high-density seabream, elevated swimming activity and respiration were accompanied by reduced energy partitioning for growth and impaired FCR, showing that more energy was diverted toward activity and coping functions rather than tissue deposition (Holhorea et al., 2023). Experimental and comparative work also shows that nutrient use depends on balancing intake with metabolic demand: protein synthesis requires both amino acids and energy, while absorbed protein and energy are under-utilized when their ratio is mismatched (Konnert et al., 2022). For L. *maculatus*, this means that feeding management should be evaluated together with farming system effects on density, oxygen, and activity, because the same diet can support either efficient growth or costly stress compensation depending on the rearing environment.

8 Case Study: Comparative Evaluation of Pond vs. Cage vs. RAS Systems in Commercial Chinese Sea Bass Farming

8.1 System design and operational characteristics

Commercial Chinese sea bass production is still centered on pond and marine net-cage culture, with pond farming especially established in the Bai Jiao area of Guangdong and cage farming concentrated in sheltered coastal waters such as Fujian (Huang et al., 2025). Pond systems are relatively simple and locally adapted, but they remain open to environmental fluctuation and disease-related microbial shifts, as shown by clear bacterial community differences between low- and high-mortality sea bass ponds (Deng et al., 2021). In contrast, cage systems use large open-water production units that increasingly approach industrial scale, and performance can change substantially with cage volume rather than density alone.

RAS differs from both pond and cage farming by replacing natural water exchange with engineered purification and near-continuous environmental control. Integrated land-based RAS can combine recirculating ponds with a primary biological pond, constructed wetlands, and ecological ditches, creating a managed treatment train rather than a single grow-out unit. Indoor RAS is also less exposed to rainfall, drought, salinity fluctuation, and other climatic disturbances than ponds or cages, although this operational stability comes with higher capital cost, higher energy demand, and greater design complexity (Ahmed and Turchini, 2021). For commercial Chinese sea bass farming, the core design trade-off is therefore between the low infrastructure burden of ponds, the spatial efficiency of cages, and the environmental controllability of RAS (Figure 2).

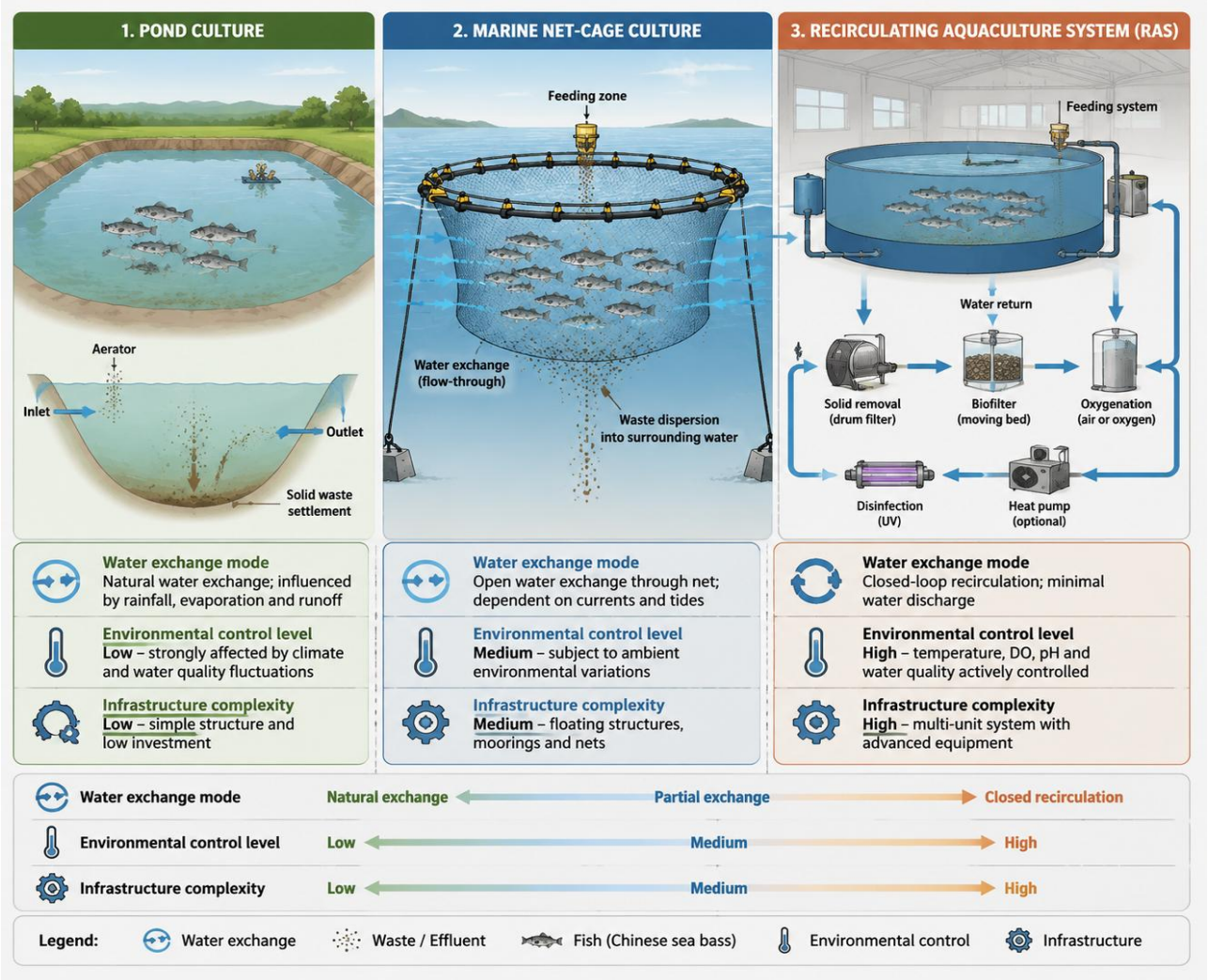

Figure 2 Comparative schematic of pond, cage, and recirculating aquaculture system (RAS) used for Chinese sea bass production, highlighting differences in water exchange mechanisms and environmental control levels

8.2 Integrated comparison of growth, survival, and FCR outcomes

Across systems, production outcomes track environmental control more closely than system label alone. In recirculating production, fish performance changed with water-quality gradients within the system, and final weight, survival rate, specific growth rate, and yield all responded to those differences. In cage production, larger rearing units produced better overall performance than the smallest cages, with higher growth rate, better FCR, and higher survival in European sea bass, which supports the view that well-scaled open-water systems can outperform undersized or stressed units. For Chinese sea bass, recent review evidence also notes that desalinated pond-reared fish can grow about one-third faster than fish reared in seawater, although this advantage is offset when high-density freshwater ponds degrade product quality (Huang et al., 2025).

A comparative case-study interpretation therefore suggests a three-way pattern. Pond systems can deliver strong growth under favorable local conditions and low capital cost, but their biological outcomes are more exposed to water-quality instability and disease-associated community shifts (Deng et al., 2021). Cage systems can support high production and good feed efficiency when cage size and site conditions are appropriate, but they remain vulnerable to environmental exposure and stress, including the typhoon risk explicitly noted for Chinese sea bass cage farming (Huang et al., 2025). RAS appears most consistent for stabilizing survival and feed use because it provides better year-round environmental conditions for water-quality-sensitive fish, and analogous bass evidence shows higher body weight in funnel-shaped recirculating systems than in traditional ponds (Xu et al., 2025).

8.3 Practical implications for system optimization and industry scaling

For system optimization, the strongest practical lesson is that each farming mode should be improved around its main constraint rather than replaced wholesale. Pond and cage systems remain commercially important because they are already embedded in China's sea bass industry, but their scaling is constrained by exposure to open-environment variability, storm risk, and site limitations (Huang et al., 2025). RAS offers a strategic pathway where land, water, pollution limits, or climate instability constrain expansion, because it is water-efficient, highly productive, and largely decoupled from external climatic shocks (Ahmed and Turchini, 2021). This makes RAS particularly attractive for high-value commercial Chinese sea bass operations targeting standardized production and secure supply.

Industry scaling, however, depends on solving operational bottlenecks rather than assuming that recirculation alone guarantees better outcomes. Interviews across the RAS sector identify poor system design and weak management capacity as major barriers, and they emphasize the need for commercial-scale equipment optimization and skilled personnel responsible for water quality and mechanical reliability. Broader sustainability reviews reach a similar conclusion: despite clear environmental advantages, RAS still contributes a small share of total production because high initial investment requires high stocking density and production to recover costs. In commercial Chinese sea bass farming, the most scalable pathway is therefore likely to be a hybrid industry structure in which ponds and cages remain dominant for lower-cost volume production, while RAS expands selectively in regions and market segments that reward tighter environmental control, product consistency, and climate resilience.

9 Integrated Strategies for Improving Farming System Efficiency

Precision aquaculture can improve the farming efficiency of Chinese sea bass by replacing intermittent manual checks with continuous measurement of critical water-quality variables such as temperature, pH, and dissolved oxygen. Real-time monitoring is especially relevant because instability in these parameters increases disease risk, mortality, and production losses, whereas IoT-based sensing allows faster detection of deteriorating conditions and more timely management responses. In *Asian seabass* farming specifically, low-cost IoT sensor platforms have already shown strong practical value, with calibrated systems achieving 76%-97% accuracy and supporting reliable real-time visualization for farm management. The next step is to connect monitoring with prediction and automated control so that environmental deviations can be corrected before they suppress growth or survival. Recent work shows that IoT systems coupled with machine learning can maintain stable water conditions, reduce mortality, and sustain survival above 90% during stressful periods, while fuzzy-logic control can autonomously regulate key variables such as dissolved oxygen and salinity to improve operational efficiency.

System hybridization offers a pathway to higher efficiency by redesigning Chinese sea bass farming systems so that wastes from fed fish become inputs for other cultured organisms. In integrated multi-trophic aquaculture (IMTA), finfish are cultured alongside extractive species such as seaweeds, mollusks, or deposit feeders, which recapture organic and inorganic nutrients, reduce waste discharge, and convert lost nutrients into additional biomass of market value. The main advantage of ecological intensification is that it can improve both environmental performance and farm diversification, but implementation depends on site design and economic feasibility. Open-water IMTA has been proposed as a way to combine biomitigation with added output from extractive crops, yet offshore settings impose technical and economic constraints, while spatially separated but ecologically linked regional IMTA may offer a more realistic model where direct co-culture is difficult in marine fish farming.

Long-term efficiency in Chinese sea bass farming depends not only on biological performance but also on economic optimization of inputs, infrastructure, and resource use. Across aquaculture systems, improved production efficiency has been associated with lower greenhouse-gas intensity, reduced land and freshwater use per unit output, and better feed management, indicating that environmental and economic sustainability often improve together rather than acting as opposing goals. Broader comparative evidence likewise shows that economic, social, and environmental outcomes are often mutually reinforced, although performance still varies substantially among production systems and leaves room for targeted innovation and investment. At the farm level, economic optimization requires matching

system choice and intensity to cost structure. Reviews of cost-benefit analysis show that production-system assessment should account for environmental externalities as well as direct financial returns, while empirical evidence from intensive aquaculture indicates that higher-performing systems can lower unit costs by spreading fixed costs across greater output, even though technologies such as RAS remain vulnerable to feed and energy prices and therefore require careful control of electricity, water, and feed use.

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Review Article Open Access

Evaluation of Sustainable Farming Models for Nori Cultivation

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Abstract As a vital marine economic seaweed in my country, *Porphyra* (nori) cultivation has expanded significantly, playing a crucial role in ensuring the supply of high-quality seaweed products and driving the development of coastal fishery economies. However, while traditional cultivation models have grown rapidly, they face challenges such as excessive stocking densities, low resource utilization efficiency, mounting environmental pressure, and accumulating ecological risks, all of which constrain the industry's sustainable development. Green cultivation models have garnered widespread attention in recent years as a key pathway for the transformation and upgrading of the *Porphyra* industry. This paper systematically reviews the theoretical foundations and technical characteristics of green *Porphyra* cultivation, focusing on the application status of typical models such as eco-friendly management, Integrated Multi-Trophic Aquaculture (IMTA), and digital intelligent cultivation. On this basis, a comprehensive evaluation indicator system-encompassing ecological, economic, and social benefits-is constructed to assess the effectiveness of green cultivation models in terms of yield and quality improvement, resource utilization optimization, environmental load reduction, and enhanced industrial competitiveness. Furthermore, using typical *Porphyra* production regions as case studies, the paper analyzes changes in ecological and economic benefits following the implementation of green cultivation technologies, summarizing experiences in their promotion and identifying existing issues. The study concludes that green cultivation models can effectively enhance the stability of cultivation systems, promote efficient resource use and ecological improvement, and achieve synergistic gains in both economic and ecological benefits. Future efforts should focus on fostering key technological innovations, refining standardized management systems, and strengthening policy support mechanisms to drive the *Porphyra* industry toward high efficiency, environmental sustainability, and long-term viability.

Keywords *Porphyra*; Green cultivation; Sustainable development; Comprehensive evaluation; Integrated multi-trophic aquaculture (IMTA); Ecological benefits

1 Intruction

Porphyra-commercially known as nori or laver-is among the most economically important cultivated seaweeds in the world, with especially strong production and consumption bases in East Asia. Modern cultivation technologies introduced since the 1960s, including artificial seeding, floating-net systems, and improved processing, enabled rapid increases in annual nori yield and helped transform *Porphyra* into a major mariculture commodity. Its market value is tied not only to production volume but also to its role as a premium edible seaweed: *Porphyra*/*Pyropia* accounts for about 8.6% of global cultivated seaweed output, and *Porphyra* species have been reported to achieve some of the highest fresh-weight values among cultivated seaweeds, reflecting their importance in food markets and aquaculture-based coastal economies (Da Silva et al., 2025).

The industry's economic significance is further reinforced by the nutritional and commercial versatility of nori. *Porphyra*, *Pyropia*, and *NeoPyropia* are widely cultivated and consumed because they combine high food value with nutraceutical potential, containing proteins, minerals, lipids, and bioactive compounds that support expanding consumer demand in both traditional and emerging markets (Da Silva et al., 2025). Historically, this value has been substantial: as early as 1992, global production reached approximately 15 billion sheets, or about 45,000 dry metric tons, with an annual value of US$1.8 billion, illustrating that nori had already developed into a high-value marine crop decades ago. Continued demand growth, together with market expansion beyond Asia, has kept nori strategically important for food supply diversification and value-added marine product development.

Despite its economic promise, traditional nori farming models face growing resource and environmental constraints that challenge long-term sustainability. Production systems are highly sensitive to environmental variability, particularly temperature, irradiance, and the availability of nitrate and dissolved inorganic carbon, all of which directly affect photosynthesis, reserve accumulation, and yield stability (Tac et al., 2025). Resource-use assessments also show that although seaweed farming is less input-intensive than many fed aquaculture systems, most impacts in *Porphyra* production are still linked to fuel use during operation and maintenance, indicating that farm design and logistics remain central sustainability concerns. In practice, traditional expansion is also limited by finite suitable farming areas, labor demands, and management constraints, factors that have contributed to stagnation in some established producing regions even as market demand continues to rise (Da Silva et al., 2025).

These pressures make the development and evaluation of green farming models an urgent research priority. Seaweed aquaculture is increasingly viewed as a nature-based production system that can contribute to food supply, climate mitigation, and eutrophication control, while avoiding some of the land and freshwater constraints that limit terrestrial agriculture (Duarte et al., 2021). For *Porphyra* specifically, cultivation can remove substantial amounts of dissolved inorganic nitrogen and phosphorus from coastal waters, showing that appropriately designed systems can generate both marketable biomass and measurable environmental services. At the same time, not all "green" models will perform equally well across ecological and economic contexts, so evaluation frameworks are needed to compare options such as low-input farming, integrated multi-trophic aquaculture, and site-optimized cultivation in terms of productivity, resilience, resource efficiency, and environmental benefit. Such evaluation is essential if nori cultivation is to move from a traditionally successful industry toward a genuinely sustainable and scalable blue-food system (Zhu et al., 2025).

2 Theoretical Basis of Green *Porphyra* Farming Models

2.1 Concepts of green aquaculture and ecological fisheries

Green *Porphyra* farming can be understood as an aquaculture model that prioritizes low external inputs, efficient nutrient use, and positive ecological functions while maintaining commercial productivity. In the broader seaweed sector, cultivation is increasingly framed as a nature-based production system because it can provide food and industrial raw materials while also contributing to carbon uptake, eutrophication mitigation, and circular bioeconomy development (Duarte et al., 2021). Ecological aquaculture extends this logic by arguing that seaweed farms should be designed to mimic the form and function of natural ecosystems and be managed as knowledge-based production systems embedded in social as well as environmental contexts (Augyte et al., 2021).

Within this framework, ecological fisheries and green aquaculture converge around the principle that farming systems should not merely reduce damage, but should actively recycle materials and generate ecosystem services. Integrated multi-trophic aquaculture is especially relevant because seaweed functions as an extractive component that assimilates dissolved nutrients released by fed species, thereby improving nutrient recycling and potentially increasing both environmental and economic performance (Lead et al., 2021; Zhu et al., 2025). For *Porphyra* cultivation specifically, this principle supports a transition from single-output farming toward ecosystem-based and restorative production models in which biomass harvest is linked to water-quality regulation and coastal ecological management.

2.2 Structure and function of the *Porphyra* farming ecosystem

The *Porphyra* farming ecosystem is structured by interactions among cultured blades, their life-history stages, surrounding water conditions, and associated microbial communities. *Porphyra* cultivation depends on a complex life cycle in which the conchocelis phase is maintained under controlled laboratory conditions before transition to blade production, making hatchery management and environmental regulation central parts of the farming system rather than auxiliary steps (García-Poza et al., 2020). Early nursery production also involves tightly managed developmental stages with controlled temperature, light, aeration, and stocking density, indicating that the farming ecosystem begins in enclosed technical environments and later expands into open-water ecological interactions (Cortez et al., 2026).

Its functional performance is governed primarily by biophysical and biogeochemical processes, especially light capture, temperature response, and nitrogen and carbon assimilation. A mechanistic model of *Porphyra* aquaculture showed that structural biomass accumulation, reserve dynamics, and blade expansion are strongly driven by temperature-adjusted carbon assimilation and nitrogen uptake, while seasonal carrying-capacity thresholds determine sustainable biomass under farming conditions (Tac et al., 2025). At the same time, farmed *Porphyra* hosts abundant and developmentally structured bacterial communities, and many associated strains show auxin-producing potential, suggesting that microbiome function may contribute to algal growth, morphogenesis, and system resilience in sustainable cultivation models (Cortez et al., 2026).

2.3 Requirements for industry transformation under sustainable development goals

Transforming the *Porphyra* industry under the Sustainable Development Goals requires moving beyond output growth toward integrated environmental, social, economic, and governance performance. Seaweed aquaculture is widely recognized as capable of contributing to food security, livelihood creation, nutrient removal, and climate-related goals, but these benefits are not automatic and depend on how production systems are regulated and scaled (Duarte et al., 2021; Spillias et al., 2022). The SDG framework is inherently cross-sectoral, so sustainable industry transformation requires alliances among producers, regulators, researchers, and communities, supported by legislation that coordinates development while protecting environmental quality and social stability (Jolly et al., 2023).

In practical terms, this transformation requires diversification, technological upgrading, adaptive governance, and value-chain development. Current research identifies species diversification, advanced cultivation technologies, digital tools, biosecurity planning, and supportive policy frameworks as necessary for sustainable seaweed sector expansion, especially where production systems remain narrow or technologically uneven. A broader industry roadmap also shows that sustainability assessment must extend beyond the conventional triple bottom line to include governance and cultural dimensions, while future growth should leverage synergies with sectors such as IMTA and offshore infrastructure to achieve economic viability without losing ecological integrity (Jueterbock et al., 2025).

3 Main Types and Technical Characteristics of Green *Porphyra* Farming Models

3.1 Ecological farming management models

Ecological farming management models for *Porphyra* emphasize low-impact production, environmental matching, and cultivation practices that align farm operation with coastal ecological processes. At the farm scale, *Porphyra* growth is strongly controlled by temperature, irradiance, and nutrient availability, and mechanistic modeling shows that carbon assimilation, nitrogen uptake, and seasonal carrying capacity are central variables for sustainable biomass management (Tac et al., 2025). This means ecological management is not simply "low input," but a strategy of regulating stocking density, harvest timing, and farm intensity to remain within environmental thresholds that support stable growth (Tac et al., 2025).

Field evidence also shows that *Porphyra* farms can provide direct ecological services when managed appropriately. Large-scale cultivation of *P. yezoensis* significantly reduced dissolved inorganic nitrogen and phosphate in open coastal waters, with reductions of 50%-94% for ammonium and 42%-67% for phosphate relative to controls, indicating strong bioremediation potential (He et al., 2008). In addition, cultivation periods were associated with elevated dissolved organic carbon and enhanced production of refractory dissolved organic matter, suggesting that ecological *Porphyra* farming can also contribute to coastal carbon sequestration functions (Wang et al., 2025).

3.2 Integrated multi-trophic aquaculture models

IMTA models incorporate *Porphyra* or other seaweeds as extractive species that recover dissolved nutrients released by fed aquaculture, converting waste into harvestable biomass. The core principle is trophic complementarity: seaweeds capture inorganic nutrients, suspension feeders use fine particulates, and deposit feeders process larger organic wastes, allowing nutrient recirculation within one farming system. Reviews of IMTA performance show that this approach can substantially retain nutrients supplied to aquaculture, with theoretical retention efficiencies of 79%-94% for nitrogen, phosphorus, and carbon, although realistic values are lower in practice because of spatial and biological constraints (Nederlof et al., 2021).

For *Porphyra*, IMTA is attractive because the genus functions as an efficient inorganic nutrient extractor while retaining commercial value as a food crop. Modeling studies indicate that macroalgal bioremediation performance depends strongly on species choice, flow regime, optical conditions, and harvest frequency, and that management can increase nutrient removal capacity by up to 25-fold. Broader reviews also note that although IMTA improves ecological balance and co-cultured species performance, long-term adoption still depends on practical issues such as seaweed selection, cultivation-area allocation, infrastructure cost, and economic evaluation rather than environmental benefit alone (Zhu et al., 2025).

3.3 Digital and intelligent green farming models

Digital and intelligent green farming models apply sensors, remote sensing, and predictive analytics to improve environmental control, crop monitoring, and harvest decisions in seaweed aquaculture. In precision aquaculture, interconnected sensors are used to monitor farm conditions and support data-driven management, and this model is increasingly framed as part of an Internet of Things architecture for sustainable aquaculture intensification. For seaweed specifically, low-power underwater devices can now log temperature, light, depth, and motion directly on cultivation structures, giving farmers continuous environmental information relevant to biomass development and farm stress (Da Silva et al., 2021).

The technical characteristic that distinguishes intelligent *Porphyra* farming is the shift from periodic manual inspection to continuous prediction and automated decision support. Drone-based multispectral monitoring has already shown that seaweed biomass and product traits can be estimated at the level of individual cultivation lines, opening a pathway toward plot-scale precision management (Nurdin et al., 2023). Likewise, IoT-based monitoring combined with physics-constrained machine learning improved biomass forecasting accuracy and can identify growth plateaus or suboptimal conditions early enough to support better harvest timing and operational adjustment (Kunapinun et al., 2024).

4 Construction of an Evaluation Indicator System for Green *Porphyra* Farming Models

4.1 Indicators for ecological and environmental benefits

Ecological and environmental indicators should measure whether *Porphyra* farming improves coastal ecosystem quality while remaining within ecological carrying capacity. In seaweed aquaculture, carrying capacity is a core concept under the Ecosystem Approach to Aquaculture because it defines the upper production limit that does not compromise ecosystem functioning, and indicator systems therefore need to track water quality, benthic effects, cultured-organism health, food-web interactions, and resource use. For green *Porphyra* models, these dimensions can be operationalized through indicators such as dissolved inorganic nitrogen and phosphorus removal, dissolved oxygen change, water transparency, sediment condition, and stocking density relative to site capacity.

Nutrient removal and carbon-related services are especially important because they capture the distinctive ecological value of seaweed farming. Large-scale seaweed aquaculture in China removed about 75,563 t of nitrogen and 9,592 t of phosphate, while also sequestering 539,555 t of carbon and absorbing 1,980,167 t of CO2, showing that nutrient extraction and carbon regulation are quantifiable environmental outputs. For *Porphyra* specifically, cultivation significantly lowered coastal nutrient concentrations and also enhanced refractory dissolved organic matter production, supporting the inclusion of nitrogen and phosphorus uptake, carbon sequestration potential, and water-column organic carbon dynamics as key indicators (Wang et al., 2025).

4.2 Indicators for economic benefits

Economic indicators should assess whether green *Porphyra* farming models can convert environmental performance into stable commercial returns. At the production level, yield, biomass quality, product standardization, and output reliability are essential because seaweed productivity and quality vary strongly with site conditions, cultivation method, and stock characteristics (Rimmer et al., 2021). Controlled land-based cultivation also shows that high-quality and standardized biomass can be produced efficiently when systems allow traceability and optimal expression of genetic potential, so evaluation should include premium-quality rate, processing suitability, and price realization as well as simple biomass output.

Profitability indicators should also capture cost structure, market resilience, and the ability to benefit from diversified value chains. Seaweed farming can become profitable when biomass sales are counted, but profitability is constrained by labor costs, annual biomass variation, immature supply chains, and limited access to space, so net profit margin, benefit-cost ratio, labor productivity, and market-channel diversity are all relevant metrics (Hasselström et al., 2020). Because continued growth depends on rising demand, output diversification, and in some settings compensation for environmental services, a complete indicator system should also include value-added product share, demand stability, and access to policy support or ecosystem-service payments.

4.3 Indicators for social benefits and industrial sustainability

Social-benefit indicators should measure how green *Porphyra* farming contributes to livelihoods, community resilience, and broader sustainable-development goals. Expert and policy-oriented assessments show that seaweed farming can support food security, decent work, economic growth, sustainable production, and multiple other SDGs, but these benefits depend on effective regulation and mitigation of negative trade-offs (Spillias et al., 2022). For this reason, social evaluation should include employment creation, household income support, participation of smallholders, contribution to local food systems, and alignment with public sustainability goals (Hossain et al., 2021).

Industrial sustainability indicators should then evaluate whether the *Porphyra* sector can remain competitive and adaptive over time. Long-term sustainability depends on improved and more consistent farm productivity, better product quality, technical support services, and diversification of value chains to reduce vulnerability to price fluctuations (Rimmer et al., 2021). Industry transformation also requires supportive governance, strategic planning, and robust value-chain coordination, so indicators such as technical extension coverage, innovation adoption, supply-chain maturity, marketing capacity, and policy support should be incorporated alongside ecological and economic measures (Yong et al., 2024).

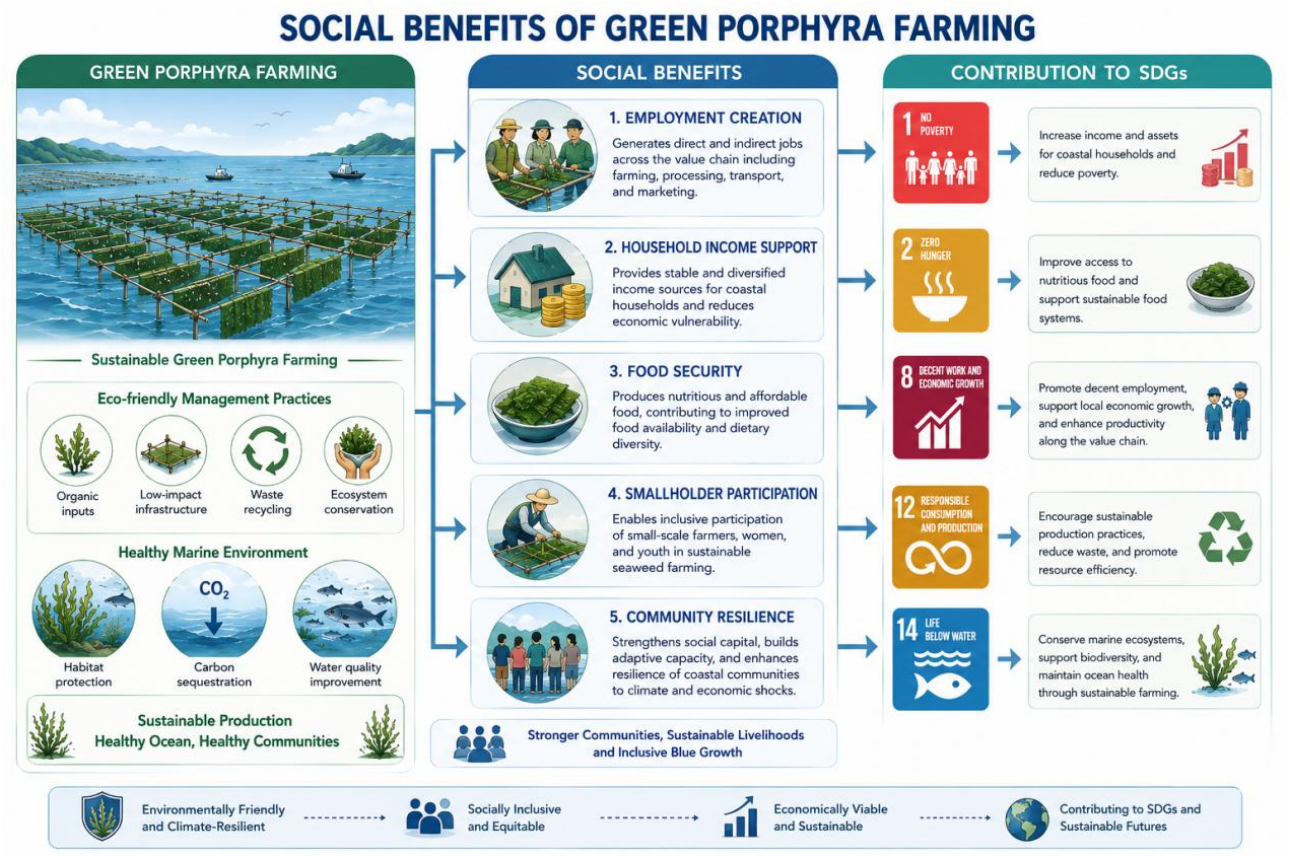

Figure 1 Conceptual pathways linking green *Porphyra* farming to social sustainability outcomes and sustainable development goals (SDGs)

5 Evaluation of the Application Effects of Green *Porphyra* Farming Models

5.1 Impact on farming yield and product quality

Green *Porphyra* farming models tend to improve yield stability by aligning cultivation intensity and harvest timing with environmental conditions that control growth. Field-based and mechanistic evidence shows that *Porphyra* biomass accumulation is strongly shaped by temperature, nutrient availability, irradiance, and stage-specific growth dynamics, so management that responds to these variables is better positioned to sustain production across the culture cycle (Lin et al., 2025). This effect is practical rather than theoretical, because seasonal thresholds for sustainable biomass and growth have already been identified in cultivation models, allowing managers to reduce overstocking and better match harvest schedules to peak biomass formation (Lin et al., 2025).

Product quality also appears to benefit when green models reduce environmental stress and improve farm management precision. In the Maine case, organically certified nori was successfully produced and marketed, showing that environmentally oriented production can support differentiated, higher-value product pathways. At the same time, unstable site conditions, disease, farming inexperience, and drought-related nitrogen depletion caused inconsistent production, indicating that green production only supports quality advantages when site selection and environmental management are robust.

5.2 Impact on resource utilization efficiency and environmental load

Green *Porphyra* farming models improve resource utilization efficiency mainly through nutrient recovery and ecosystem-based purification. Large-scale *P. yezoensis* cultivation in Jiangsu significantly reduced ambient inorganic nutrient concentrations, with ammonium, nitrite, nitrate, and phosphate all lower in the cultivation season than in non-cultivation periods, confirming that the crop efficiently converts dissolved nutrients into harvestable biomass (He et al., 2008). Harvested biomass also removed substantial amounts of nitrogen and phosphorus from the water, directly linking production output to nutrient extraction rather than to feed or fertilizer input (He et al., 2008).

These environmental gains extend beyond nutrient removal to broader reductions in coastal environmental load. At the national scale, seaweed aquaculture in China removed 75,563 t of nitrogen and 9,592 t of phosphate from coastal waters in 2015, while also sequestering carbon and reducing the need for chemical fertilizers and pesticides compared with land-based vegetable production. *Porphyra* cultivation also appears to support carbon-focused resource efficiency, because cultivation zones showed higher dissolved organic carbon and a 169% higher estuarine addition of microbially sourced humic-like C3 during the farming period, consistent with enhanced transformation of organic matter into more refractory carbon pools (Wang et al., 2025).

5.3 Impact on farming profitability and industrial competitiveness

Green *Porphyra* farming models can strengthen profitability when environmental services are translated into lower input intensity, improved market positioning, or greater resilience. Resource-use analysis in southeastern China found that *Porphyra* production had a mean exergy demand of 0.98 GJ eq. per live-weight ton, much lower than major animal mariculture products, suggesting an inherent efficiency advantage that can support competitive production if farm operations and fuel use are well managed. However, 83%-99% of seaweed-production impacts were linked to fuel used in operation and maintenance, so green competitiveness depends heavily on farm design, logistics, and spatial planning rather than on biology alone.

Industrial competitiveness also improves when green *Porphyra* farming is embedded in broader blue-economy value creation. China's seaweed cultivation has been framed as a sustainable mariculture model with ecological and economic benefits, including major contributions to carbon sequestration and blue-carbon development, which can expand the industry's strategic value beyond food production alone (Wang et al., 2025). Even so, evidence remains mixed on how easily environmental benefits convert into farm-level profits, because regional water quality, species selection, and management intensity still require spatial adjustment, and poorly matched farming layouts can reduce both ecological and economic performance.

6 Case Study: Application of a Sustainable Nori Farming Model

6.1 Overview of the case study area and farming model design

The case study area can be framed as a nutrient-influenced coastal zone suitable for *Porphyra*/*Pyropia* cultivation, with model design guided by the dual goals of biomass production and environmental service delivery. Seaweed aquaculture is already recognized as a large and growing component of global mariculture, and it is increasingly valued for climate mitigation, eutrophication control, and broader circular-bioeconomy functions (Duarte et al., 2021). For nori specifically, site suitability depends strongly on temperature, irradiance, and nutrient availability, because these drivers regulate photosynthesis, reserve accumulation, and final yield under field conditions.

Accordingly, the farming model was designed as a seasonal, ecosystem-based production system that combines offshore or nearshore cultivation with controlled nursery support and adaptive capacity limits. Early-stage *Porphyra* production is commonly stabilized in indoor nurseries where stocking density, temperature, light, and aeration are controlled before scale-up (Cortez et al., 2026). At the farm scale, sustainable layout also requires matching cultivation density to environmental carrying capacity and using scenario-based planning tools that can forecast biomass performance under changing field conditions (Tac et al., 2025).

6.2 Implementation of sustainable farming techniques and management measures

Implementation centered on three linked measures: controlled seedling production, nutrient-efficient cultivation, and integrated environmental management. Nori cultivation is inherently challenging because of its heteromorphic life cycle, so reliable hatchery control over the conchocelis, spore, and young blade stages is essential for stable commercial output (Cortez et al., 2026). Where full conchocelis control is difficult, simplified propagation pathways such as neutral-spore-based culture can reduce technical barriers and support low-cost local expansion of *Pyropia* farming.

Field management emphasized water-quality regulation, spacing, and timing in order to maximize nutrient uptake while limiting stress and crop quality loss. Large-scale *Porphyra* cultivation in open coastal waters has been shown to reduce dissolved inorganic nitrogen and phosphorus substantially, with reported reductions of 50%-94% for ammonium and 42%-67% for phosphate relative to controls (He et al., 2008). Because farming outcomes are highly site-specific, operational practices such as net depth, seeding timing, and periodic exposure or other anti-fouling measures must be adjusted to local current, light, temperature, and water-quality regimes rather than transferred unchanged across sites.

6.3 Analysis of application results and summary of experience

The application results indicate that a sustainable nori farming model can generate both production and ecological gains when cultivation intensity is aligned with local environmental conditions. *Porphyra* farming can function as an extractive component in integrated multi-trophic aquaculture, recycling excess nutrients and improving the environmental performance of aquaculture sites while adding total biomass value. More broadly, seaweed cultivation in China has been estimated to remove large nutrient loads and sequester substantial carbon, although the magnitude of benefits depends on spatial management and local water quality.

The main lessons from the case study are that sustainable nori farming depends on adaptive site selection, biological risk management, and realistic economic planning rather than on yield maximization alone. Long-term resilience requires attention to disease, pests, governance, and climate-related stressors, because short-term success can be undermined if environmental and operational risks are underestimated (Zhu et al., 2025). It also requires protecting genetic resources and avoiding overly narrow cultivation bases, since reduced diversity and unmanaged farm-wild interactions can weaken resilience over time (Brakel et al., 2021).

7 Challenges in Promoting Green *Porphyra* Farming Models

7.1 Insufficient technology integration and standardization

A central constraint on promoting green *Porphyra* farming models is that many enabling technologies remain fragmented rather than integrated into standardized production systems. Reviews of seaweed aquaculture show that

sustainable expansion depends on combining site selection, cultivation engineering, environmental monitoring, breeding, and biosecurity into coherent farm-management frameworks, yet current development is still characterized by uneven technical adoption and unresolved operational bottlenecks (Khan et al., 2024). This fragmentation is especially important for *Porphyra*, because cultivation performance depends on jointly managing environmental variability, seasonal growth dynamics, and infrastructure design rather than optimizing any single component in isolation (Sen et al., 2025).

Standardization is also limited by the diversity of cultivation environments and control methods used across farms. For *NeoPyropia*/*Pyropia* culture, fixed-pole, floating, and semi-floating raft methods are all used, while epiphyte control can rely on desiccation or pH treatment, indicating that operational practices remain heterogeneous and not yet fully harmonized into common green-production standards (García-Poza et al., 2020). More broadly, seaweed farming studies stress that economically and ecologically sustainable production requires state-of-the-art but practical methods, along with country-specific standards and monitoring protocols, which suggests that green *Porphyra* farming still lacks sufficiently unified technical norms for large-scale replication (Khan et al., 2024).

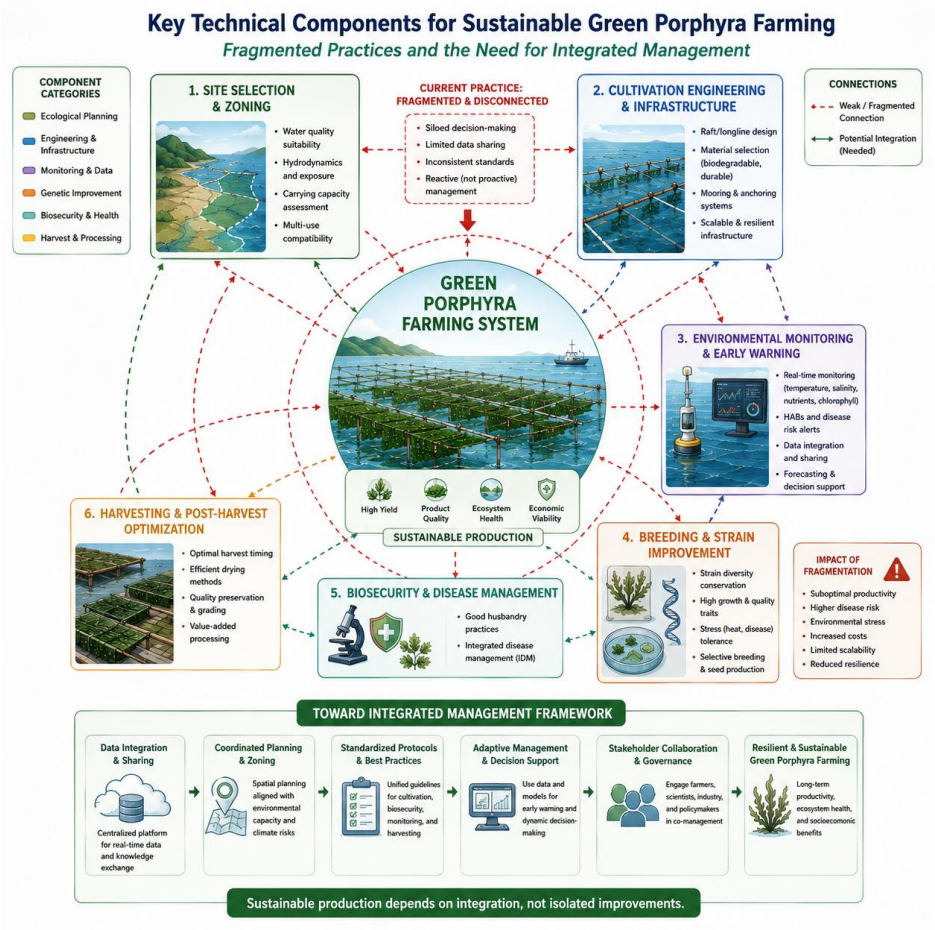

Figure 2 Conceptual framework illustrating the fragmented technological components involved in green *Porphyra* farming systems

7.2 Disparities in awareness and management capabilities among farming entities

A second challenge is the uneven awareness, technical knowledge, and management capacity among different farming entities. Evidence from broader seaweed aquaculture shows that farmers need access to educational programs, technical support, and affordable planting materials and equipment to manage threats and production risks effectively, implying that green transitions are constrained where training and extension systems are weak (Khan et al., 2024). This matters because the sustainable development of aquaculture increasingly depends on integrating technical, environmental, and governance knowledge, yet progress is uneven across producer groups and regions (Mair et al., 2023).

Capability gaps also appear in the ability to respond to biotic and abiotic stressors. Seaweed yield is highly sensitive to temperature, salinity, light, nutrient availability, pests, and disease, so farms with weaker monitoring and management capacity are less able to maintain stable output under changing conditions (Khan et al., 2024). Reviews further emphasize that careful site selection, development of disease-resistant strains, and improved mitigation strategies are essential for overcoming these pressures, which means disparities in management competence directly translate into disparities in green-farming performance (Khan et al., 2024).

7.3 Need for improvement in market mechanisms and policy support systems

Green *Porphyra* farming also faces a structural challenge in that market mechanisms often do not fully reward ecological performance. Seaweed aquaculture delivers ecosystem services such as climate mitigation, eutrophication control, and circular-bioeconomy benefits, but these benefits do not automatically translate into farm-level returns unless value chains, product markets, and institutional incentives are aligned (Duarte et al., 2021). Even when seaweed farming is environmentally cost-effective, long-term industry growth still requires rising demand, output diversification, and some form of compensation or policy recognition for nutrient-removal services (Khan et al., 2024).

Policy support systems also remain incomplete relative to the scale of transformation required. Efficiency analyses of China's seaweed sector indicate that green development has improved, but significant regional disparities persist and future progress depends on technology innovation, structural optimization, carbon-sink trading policy, and specialized talent development (Le and Wei, 2023). At the global level, sustainable aquaculture roadmaps similarly stress stronger governance, regulatory frameworks, research investment, and planning integration, indicating that green *Porphyra* farming will advance fastest where market design and public policy evolve together rather than separately (Mair et al., 2023).

8 Conclusions and Future Outlook

Overall, green *Porphyra* farming models have shown clear application value because they combine biomass production with measurable ecological services. Open-sea cultivation of *P. yezoensis* significantly reduced dissolved inorganic nitrogen and phosphorus, demonstrating that nori farming can function as an effective bioremediation system in eutrophic coastal waters. At the broader seaweed-aquaculture level, seaweed farming is recognized as a nature-based pathway for climate mitigation, eutrophication control, and circular bioeconomy development, which reinforces the strategic value of green *Porphyra* models beyond simple yield enhancement.

The effectiveness of these models is also reflected in their contribution to carbon-related ecosystem functions, although the strength of evidence differs by mechanism. Recent field evidence shows that *Porphyra* cultivation increased dissolved organic carbon and promoted refractory dissolved organic matter formation, indicating a positive role in coastal carbon sequestration processes. At the same time, national-scale analysis in China found that seaweed cultivation has already generated substantial CO_2-emission reduction and blue-carbon benefits, supporting the view that green nori farming should be evaluated as part of a larger low-carbon mariculture transition rather than as an isolated farm technology.

Future progress in green *Porphyra* farming will depend first on strengthening breeding and production-control technologies. Across seaweed aquaculture, breeding and genetic improvement are identified as priorities for developing strains that are more productive, stress resistant, and better suited to climate change, while recent reviews also point to tissue culture, selective breeding, and gene-editing approaches as promising tools to improve yield, stress tolerance, and biochemical traits. For *Porphyra* specifically, this direction is important because strain performance under warming, nutrient fluctuation, and disease pressure will increasingly determine the real effectiveness of green farming systems.

A second technology direction is the integration of intelligent monitoring, automation, and advanced environmental management. Reviews of seaweed farming emphasize automated cultivation and harvesting systems as a route to higher efficiency and lower cost, while Industry 4.0 analyses show that digitalization is becoming a core pathway

for improving seaweed aquaculture techniques and management precision. In parallel, nanosensors and related monitoring tools are being proposed for water-quality surveillance, disease detection, and biofouling control, suggesting that future green *Porphyra* models will increasingly rely on real-time sensing and early-warning capacity rather than periodic manual observation alone.

The high-quality development of the *Porphyra* industry will require moving from farm-level greening to whole-industry coordination across governance, markets, and value chains. Global aquaculture assessments emphasize that sustainable growth depends on stronger governance, regulatory frameworks, social responsibility, and greater investment in research and development, while China's green-aquaculture framework likewise defines green development as the joint achievement of environmental friendliness, technical efficiency, product safety, income growth, and consumer satisfaction. This means that the future of the nori industry should not be judged only by production expansion, but by whether ecological, economic, and product-quality goals are advanced together.

A second pathway is to build a more diversified and resilient blue-economy structure around *Porphyra* biomass. Recent reviews indicate that *Porphyra* has expanding potential in food, pharmaceuticals, nutraceuticals, and biofuel applications, while broader seaweed outlooks argue that scaling seaweed aquaculture is essential for food security and sustainability under future resource constraints. In this sense, the long-term outlook for green *Porphyra* farming is strongest when the industry links high-standard cultivation with value-added processing, ecosystem-service recognition, and low-carbon development pathways.

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Feature Review Open Access

Adaptation Strategies for Kelp Farming Under Climate Change

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Abstract Climate change is increasingly challenging the sustainability and productivity of kelp farming through ocean warming, marine heatwaves, ocean acidification, extreme weather events, and shifts in nutrient availability. This paper systematically reviews adaptation strategies for enhancing the resilience of kelp farming under changing marine environmental conditions. It first examines the physiological, genetic, and ecological responses of kelp to major climate stressors, with particular emphasis on thermal tolerance, photosynthetic regulation, oxidative stress, genetic diversity, and ecological interactions. The paper then evaluates adaptive cultivation and farm management strategies, including optimized site selection, seasonal production adjustment, cultivation-depth regulation, stocking-density management, and environmental monitoring. Biological and technological approaches, such as selective breeding, controlled hatchery production, genomics, transcriptomics, and microbiome-based research, are further discussed for developing climate-resilient kelp strains. Integrated multi-trophic aquaculture and climate-smart management are highlighted as ecosystem-based approaches for improving resource-use efficiency and reducing production risks. A representative case study is proposed to evaluate the practical implementation and effectiveness of regional adaptation measures. Finally, the integration of artificial intelligence, remote sensing, predictive modeling, and digital monitoring is discussed as an important pathway toward intelligent and climate-resilient kelp aquaculture.

Keywords Kelp farming; Climate change; Climate adaptation; Thermal stress; Sustainable aquaculture

1 Introduction

Anthropogenic climate change is reshaping the marine environment through rising atmospheric CO_2, ocean warming, acidification, altered salinity regimes, and more frequent extreme events. Atmospheric CO_2 has increased from about 280 ppm in the pre-industrial era to 420 ppm, and much of the resulting excess heat has been absorbed by the ocean, driving persistent changes in sea temperature and seawater chemistry (Veenhof et al., 2024). These changes are especially consequential for kelps because their physiology, reproduction, and geographic distribution are tightly linked to temperature and other environmental controls. Across temperate and polar systems, warming trends and marine heatwaves are associated with reduced kelp growth and survival, disrupted recruitment, and poleward shifts or contractions at warm range edges, while interacting stressors such as sedimentation, deoxygenation, and freshwater inputs can intensify local impacts. As a result, climate change is no longer a distant background pressure for kelp cultivation but an immediate oceanographic reality that is redefining where, when, and how kelp can be farmed successfully (Roethler et al., 2025).

Against this environmental backdrop, kelp aquaculture has become one of the most important sectors of global marine biomass production and a strategically valuable component of the blue economy. Seaweed aquaculture accounts for more than half of global mariculture production and continues to expand, while cultivated kelps such as *Saccharina japonica* and *Undaria pinnatifida* remain among the most economically important macroalgal crops worldwide (Duarte et al., 2021; Hu et al., 2021). In production terms, kelp farming is still concentrated overwhelmingly in Asia, especially China, where industrial-scale cultivation has shaped global supply, technology development, and germplasm resources. Beyond its role as a food and hydrocolloid feedstock, kelp farming is increasingly valued for broader ecosystem services and industrial applications, including nutrient removal, habitat provision, carbon uptake, and use in bioenergy and biorefinery pathways. This combination of commercial output and ecological co-benefits explains why kelp cultivation is now widely viewed not only as an aquaculture activity,

but also as a multifunctional system with relevance to food security, circular bioeconomy development, and coastal sustainability transitions (Ross et al., 2023).

However, the same climate pressures that elevate the strategic value of kelp farming also expose serious vulnerabilities across the production cycle. Ocean warming can reduce biomass yield, alter biochemical composition, and impair reproduction, while marine heatwaves, storms, disease outbreaks, and herbivory create episodic but sometimes severe losses for farms and nurseries (Veenhof et al., 2024). These risks are compounded by declining germplasm quality, genetic contamination between cultivated and wild stocks, and uncertainty about how multiple stressors interact across microscopic and macroscopic life stages. Evidence from kelp-focused syntheses shows that warming has broadly negative effects on growth, reproduction, and survival across life stages, whereas responses to acidification alone are often weaker or more variable; importantly, combined warming and acidification can act synergistically, and impacts tend to intensify with stronger or longer exposure (Roethler et al., 2025). For the kelp aquaculture industry, this means that climate change threatens not only farm productivity, but also the biological reliability of seedstock, seasonal scheduling, and the spatial suitability of traditional cultivation grounds.

These challenges make adaptation research a central requirement for the future of kelp aquaculture rather than a secondary management option. Recent literature points to several promising directions, including future-proof site selection, development of stress-resistant cultivars, selective breeding informed by thermal tolerance and genetic diversity, microbiome-based resilience strategies, and cultivation models that integrate production with restoration or broader ecosystem management (Hu et al., 2021; Veenhof et al., 2024). Experimental work further suggests that heat-tolerant genotypes can perform better under warm farming conditions, although preserving broader genetic diversity remains essential for long-term adaptability (Harden et al., 2024). At the same time, integrated planning that accounts for climate exposure, stakeholder conflicts, and ecosystem carrying capacity is needed to avoid maladaptation and sustain both livelihoods and surrounding coastal ecosystems. Accordingly, studying adaptation strategies for kelp farming under climate change is significant not only for safeguarding yields, but also for supporting resilient coastal economies, maintaining ecosystem services, and enabling kelp aquaculture to contribute credibly to sustainable development under rapidly changing ocean conditions.

2 Mechanisms of Climate Change Impacts on Kelp Aquaculture

2.1 Effects of rising seawater temperatures on kelp growth and development

Rising seawater temperature directly constrains kelp growth because kelp performance is strongly temperature dependent, with reduced growth above species-specific optima and lower net energy gain when respiration rises faster than photosynthesis (Simonson et al., 2015). Across a global synthesis of 143 experimental studies, ocean warming showed a consistently negative effect on kelps at all life stages, impairing growth, reproduction, and survival, which indicates that warming is not a narrow local problem but a general mechanism of production risk for kelp aquaculture (Roethler et al., 2025). For farms, this means that elevated background temperatures can depress biomass accumulation over an entire production cycle while also making crop performance more sensitive to exposure intensity and duration.

Thermal stress also acts through damage to tissue integrity and early development, thereby reducing both standing biomass and recruitment success. In juvenile *Macrocystis pyrifera*, simulated marine heatwaves reduced mean growth rates by more than 30% even at moderate heatwave intensities, while 22°C caused bleaching, blade erosion, reduced chlorophyll fluorescence, and mortality (Bunting et al., 2024). Microscopic stages are especially vulnerable: in bull kelp, gametophyte densities declined sharply at 18°C, 20-22°C was lethal, and sporophyte production was greatly reduced at 16°C-18°C, narrowing the temperature window for successful recruitment.

2.2 Effects of ocean acidification on physiological metabolism and quality formation

Ocean acidification affects kelp mainly through altered carbon chemistry, but its biological consequences are more variable than those of warming because many kelps can use bicarbonate efficiently through carbon-concentrating mechanisms. In *Macrocystis pyrifera*, elevated pCO_2 and reduced pH did not change growth or photosynthetic rates over a 7-day incubation, and this stability was linked to continued reliance on HCO3- uptake and sustained carbonic

anhydrase activity (Fernández et al., 2015). A recent global meta-analysis similarly found that ocean acidification generally had no overall effect on kelps except for a negative effect on reproduction, indicating that physiological metabolism in farmed kelps may often remain comparatively stable under acidification alone, while reproductive output remains a key vulnerability (Roethler et al., 2025).

Even so, acidification can still influence quality formation indirectly by modifying photosynthesis-respiration dynamics and by interacting with diel pH variability or other climate drivers. In *Ecklonia radiata*, pH fluctuations enhanced juvenile growth and photosynthesis under present-day mean pH, but this advantage disappeared or reversed when mean pH was reduced by 0.3 units, suggesting that future acidification may erode favorable local carbonate dynamics that currently support productivity (Britton et al., 2016). More broadly, responses of marine photosynthetic organisms to acidification depend on concurrent warming, light, nutrient supply, and oxygen conditions, and combined stressors can be synergistic, neutral, or antagonistic, which means kelp quality traits should not be interpreted from acidification-only experiments in isolation.

2.3 Effects of extreme weather events on aquaculture system stability

Extreme weather events affect kelp aquaculture not only biologically but mechanically, because farms depend on ropes, rafts, anchors, and other structures that remain exposed to waves, surge, and rapid hydrodynamic forcing. Aquaculture in general is inherently vulnerable to climate change because it relies heavily on the ambient environment, and major climate-related stressors include extreme weather, surge-based flooding, and shifts in temperature, salinity, and dissolved oxygen. The severity of impact depends on where the stress falls relative to tolerance limits, its duration over the production cycle, and the interaction of multiple simultaneous stressors, so identical storm events can produce very different outcomes across farms, species, and life stages.

For exposed marine systems, storm waves are a direct pathway to infrastructure failure and crop loss. Quantitative risk assessment in the northern East China Sea showed that tropical cyclone-induced extreme waves can destabilize aquaculture structures and generate spatially concentrated high-risk zones, underscoring the need for wave-resilient farm design and hazard mapping (Fang et al., 2025). Empirical evidence from other aquaculture sectors points in the same direction: in Türkiye, storms and flash floods accounted for 56.5% of escape incidents, while in coastal Vietnam floods and typhoons caused measurable losses of income and initial investment, demonstrating that extreme events can rapidly convert climate exposure into operational and economic instability (Lam et al., 2024; Bal and Dürrani, 2025).

3 Physiological and Ecological Responses of Kelp to Climate Change

3.1 Changes in photosynthesis and carbon fixation capacity

Ocean warming generally depresses kelp photosynthetic performance and carbon fixation, while ocean acidification alone often provides little compensation. A global meta-analysis across 143 experimental studies found that warming negatively affects kelps across life stages and physiological functions, whereas acidification usually has no effect except on reproduction (Roethler et al., 2025). Species-level experiments are consistent with this pattern: in *Ecklonia radiata*, elevated CO_2 increased photosynthesis near the thermal optimum but did not improve growth, indicating that additional dissolved CO_2 is unlikely to offset warming-induced performance losses (Britton et al., 2024).

The consequences extend from individual physiology to ecosystem carbon cycling. Along a natural temperature gradient in NE Atlantic Laminaria hyperborea forests, kelp in warm regimes assimilated more than three times less carbon and exported less than half as much particulate carbon as kelp in colder regimes, implying substantial climate-driven weakening of blue-carbon function (Pessarrodona et al., 2018). Community reorganization further amplifies this loss: marine heatwaves favor shifts from canopy-forming kelps to turf assemblages, and such structural change reduces long-term carbon sequestration potential in coastal systems (Gao et al., 2021).

3.2 Regulatory mechanisms for nutrient uptake and energy allocation

Climate change alters nutrient regulation by disrupting the tight coupling between carbon metabolism, nitrogen assimilation, and growth. In *Macrocystis pyrifera*, nitrate availability modulated thermal plasticity, buffering the

negative effects of high temperature on growth and photosynthesis during short-term exposure, which indicates that nutrient status directly regulates acclimatory capacity under warming (Fernández et al., 2020). However, this buffering has limits, because supra-optimal warming can override nutritional benefits and produce metabolic stress even when nitrogen is available (Fernández et al., 2020; Fales et al., 2023).

Recent studies also show that nitrogen and phosphorus pathways respond differently to warming, revealing important trade-offs in energy allocation. In juvenile *Saccharina latissima*, nitrate uptake declined significantly at and above 15.7°C, whereas phosphate uptake remained positive across most treatments and even became decoupled from nitrate behavior at high temperature, suggesting distinct regulatory mechanisms for N and P metabolism (Ding et al., 2025). Under phosphorus deficiency combined with thermal and high-light stress, cultivated *Saccharina japonica* first suppressed metabolism to conserve resources, then activated energy, amino acid, and coenzyme pathways under compound stress, showing a shift from metabolic conservation to compensatory energy mobilization (Zhang et al., 2025).

3.3 Changes in stress resistance and environmental adaptability

Kelp stress resistance under climate change depends on both immediate physiological tolerance and the capacity for recovery after extreme events. In juvenile *Macrocystis pyrifera*, short marine heatwave exposure caused oxidative damage, reduced growth, and lowered photosynthetic capacity, but removal of the heat stress allowed partial physiological recovery, indicating some short-term resilience (Umanzor et al., 2021). Even so, when warming coincided with nitrate scarcity, damage to photosynthetic capacity became irreversible, highlighting that multiple stressors sharply reduce recovery potential (Umanzor et al., 2021).

Environmental adaptability also varies strongly among populations and species, implying that climate responses cannot be generalized across farming regions or target taxa. Genomic analysis of *Ecklonia radiata* revealed adaptive variation linked to temperature and light, but also predicted substantial future genotype-environment mismatch under climate change, suggesting that natural adaptation may not keep pace with warming. At the same time, experiments on Arctic kelp communities found comparatively high tolerance to short-term warming and marine heatwaves, although some species still showed reduced quantum yield or net photosynthesis, demonstrating that resilience is real but species-specific rather than universal (Lebrun et al., 2025).

4 Key Technical Strategies for Climate Change Adaptation in Kelp Aquaculture

4.1 Breeding of new heat-tolerant and stress-resistant varieties

Breeding heat-tolerant and stress-resistant kelp varieties is a primary adaptation strategy because warming has strong negative effects on kelp growth, reproduction, and survival across life stages, while tolerance varies substantially among genotypes and populations (Alsuwaiyan et al., 2021; Roethler et al., 2025). Early life-stage experiments in *Ecklonia radiata* further show significant genotype-by-environment interactions under marine heatwave conditions, indicating that some genotypes are consistently more resistant and could be used as broodstock for selective breeding (Alsuwaiyan et al., 2021).

Population-level variation also supports targeted breeding for aquaculture resilience. In *Macrocystis pyrifera*, geographically isolated populations differ in thermal tolerance and nitrogen storage capacity, showing that locally adapted physiological traits already exist within cultivated or cultivable kelp germplasm (Fernández et al., 2020). However, breeding solely for heat tolerance can narrow adaptive potential, so improvement programs should combine resistant genotypes with broader genetic diversity to preserve long-term resilience under variable future stressors (Alsuwaiyan et al., 2021).

4.2 Optimization of farming zones and spatial layout adjustments

Climate adaptation also depends on moving cultivation toward locations where thermal, light, and nutrient conditions remain within kelp performance windows. Warm climatic regimes in the NE Atlantic support more than threefold less carbon assimilation and less than half the particulate carbon donation of cold regimes, indicating that site temperature strongly shapes kelp productivity and should guide farming-zone selection. At smaller scales,

increased turbidity can reduce kelp productivity by 95%, so spatial layout must account not only for temperature but also for water clarity and light penetration (Blain et al., 2021).

Spatial adjustment within farms can also buffer compound stress. Experiments on northeast Atlantic kelps showed that summertime marine heatwaves caused major declines in biomass and photosynthetic efficiency under low light, whereas the same species were largely resistant under high-light conditions, suggesting that layout choices affecting depth, shading, and water clarity can materially alter resilience. Because kelp responses vary across populations and environments, farming zones should be matched to locally appropriate genotypes rather than assuming uniform performance across regions (Fales et al., 2023).

4.3 Intelligent monitoring and precision aquaculture management technologies

Intelligent monitoring is increasingly necessary because kelp responses to climate change depend on multiple interacting stressors rather than temperature alone. Recent work on cultivated *Saccharina japonica* identifies major knowledge gaps in tolerance thresholds, metabolic trade-offs, and compensatory acclimation under combined stressors, and explicitly proposes real-time monitoring systems and machine-learning forecasting as adaptation tools for kelp aquaculture (Zhang et al., 2025). Precision fertilization is another recommended approach, because nutrient optimization can reduce deficiency stress without worsening eutrophication risk (Zhang et al., 2025).

Precision management is especially important because nutrient and temperature effects interact in complex ways. In juvenile *Saccharina latissima*, nitrate uptake declines sharply at or above 15.7°C and can shift to nitrate release at high temperatures, while phosphate uptake remains positive, showing that warming disrupts nutrient regulation in ways that require continuous monitoring rather than static farm schedules (Ding et al., 2025). Short-term experiments in *Nereocystis luetkeana* and *Saccharina latissima* likewise show that elevated temperature reduces growth and causes metabolic stress even when nitrogen is available, reinforcing the need for integrated sensor-based management of heat and nutrient conditions during cultivation (Figure 1) (Fales et al., 2023).

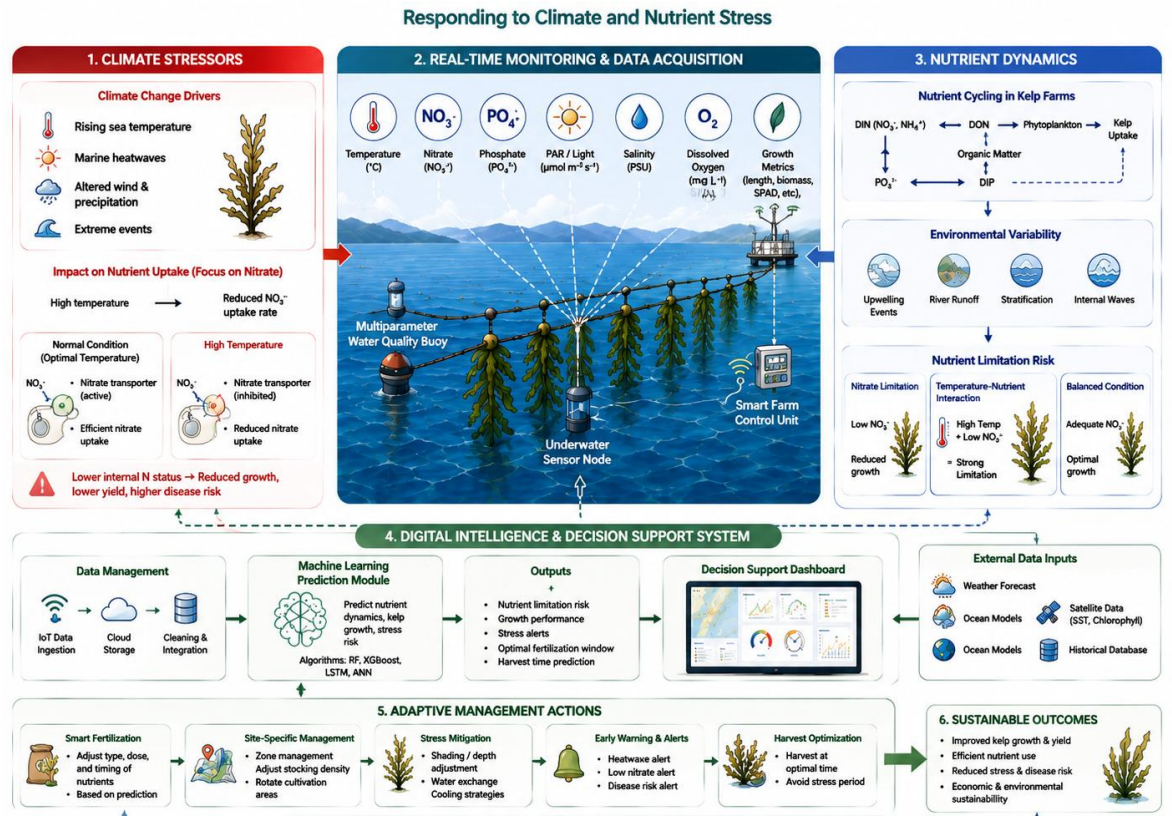

Figure 1 Integrated smart monitoring and decision-support framework for kelp (*Saccharina* spp.) aquaculture under combined climate and nutrient stressors

5 Ecological Adaptation and Integrated Management Strategies for Kelp Aquaculture

5.1 Establishment of multi-trophic integrated aquaculture models

Integrated multi-trophic aquaculture (IMTA) is a core ecological adaptation strategy for kelp farming because it couples kelp with fed or extractive species to recycle dissolved and particulate wastes, thereby improving the environmental performance of aquaculture systems under climate stress (Troell et al., 2009). Reviews of IMTA consistently describe seaweed, especially kelp, as the inorganic extractive component that can increase sustainability by converting nutrient effluents into additional biomass and co-products rather than allowing those nutrients to accumulate locally (Zhu et al., 2025).

For kelp aquaculture, the practical value of IMTA lies in both biogeochemical buffering and production diversification. In land-based integrated systems, seaweed raised mean seawater pH by 0.2 units and improved juvenile abalone growth by 22% in weight and 11% in shell area, showing that macroalgae can partially buffer acidification stress for co-cultured species (Hamilton et al., 2022). At larger commercial scales, Sanggou Bay demonstrates that IMTA can operate across whole coastal landscapes, with more than 30 species and over 240,000 t of annual seafood production, although adaptive management still depends on better understanding interactions among species, nutrient cycling, and surrounding environmental conditions.

5.2 Ecological restoration and environmental regulation measures

Ecological adaptation in kelp aquaculture should extend beyond farm production to the restoration and protection of surrounding kelp ecosystems, because farmed kelp does not reliably replace the biodiversity functions of natural kelp forests. Evidence to date indicates that kelp farms can create structured habitat and support distinct assemblages, but they typically form novel habitats rather than ecological equivalents of wild kelp forests (Forbes et al., 2022). This makes restoration and conservation of natural kelp habitats a parallel priority, especially as kelp forests are declining globally and their loss reduces biodiversity, primary production, nutrient cycling, and other ecosystem services.

Environmental regulation measures should therefore combine nutrient management, preventive conservation, and ecosystem-based governance. Field evidence from eutrophic Xiangshan Bay showed that kelp cultivation reduced dissolved inorganic nitrogen and phosphorus and removed an estimated 297 t of nitrogen and 42 t of phosphorus annually through harvest, confirming its utility as a bioremediation tool when deployed at appropriate scale (Jiang et al., 2020). At the same time, kelp ecosystem management is most effective when it follows ecosystem-based principles such as biologically relevant monitoring, cumulative-impact assessment, cross-scale governance, rapid adaptive management, and protection of food-web structure (Hamilton et al., 2022).

5.3 Risk early-warning and disaster emergency management systems

Risk early-warning systems are a necessary adaptation measure because climate change is increasing exposure to heatwaves, storms, low-oxygen events, and disease risks across aquaculture sectors. Climate risk assessment frameworks for aquaculture already identify temperature sensitivity, flooding and storm surge exposure, low-oxygen hazard, and disease vulnerability as major risk dimensions that can be evaluated in advance to support targeted adaptation planning. For kelp aquaculture, this implies that farm management should move from reactive loss response toward routine hazard mapping, threshold setting, and preparedness planning tied to local environmental drivers (Masanja et al., 2024).

Operationally, effective warning systems depend on integrating forecasts with local sensor observations and clear communication pathways. Recent aquaculture applications show that model-sensor systems can forecast farm water temperature up to 120 h ahead with errors below 2°C for up to 72 h, enabling precautionary measures before extreme temperature damage occurs (Li et al., 2024). IoT- and AI-based warning platforms have also predicted water-quality conditions 72 h in advance with 91.22% accuracy and delivered alerts through web and SMS interfaces, suggesting a practical template for kelp farming emergency systems that link monitoring, rapid communication, and farm-level response actions.

6 Case Study: Climate Adaptation Practices in Typical Kelp Farming Regions

6.1 Overview of the case study region and climate change characteristics

China, especially its northern production centers such as Shandong and Liaoning, remains the world's largest kelp farming region and therefore offers the clearest case for examining climate adaptation in commercial cultivation. At the same time, newer farming regions in the North Atlantic, such as Maine and Scandinavia, are increasingly important because they combine rapid industry expansion with strong exposure to changing coastal conditions. Across these regions, warming, shifting seasonality, and growing environmental variability are now central constraints on farm productivity and planning (Hu et al., 2021).

Climate risk is not limited to gradual warming. Evidence from China shows that *Saccharina japonica* is already among the most thermally sensitive cultivated macroalgae, and projected warming under future emissions scenarios is expected to increase heat stress across many aquaculture zones. Broader synthesis across kelp systems also shows that ocean warming reduces kelp growth, reproduction, and survival across life stages, while combined warming and acidification often intensify these effects (Roethler et al., 2025).

In practice, climate impacts also emerge through indirect and region-specific pathways. In Sanggou Bay, anomalous environmental change was linked to microbiome disruption and disease outbreaks in farmed kelp, indicating that climate stress can amplify biological hazards rather than acting only through physiology. On Canada's Pacific coast, marine heatwaves advanced bryozoan outbreaks on giant kelp, showing that warming can shift the timing and severity of epibiotic pressure in ways relevant to harvest scheduling and site choice (Zhang et al., 2024; Denley et al., 2025).

High-latitude and offshore-facing regions are not insulated from these threats. Reviews from the northeast Pacific indicate that future kelp performance will be shaped not only by temperature, but also by salinity, sediment load, and light, with important gaps remaining for vulnerable microscopic stages. More generally, ocean warming has already altered the structure and distribution of kelp ecosystems in many parts of the world, even though some populations remain locally stable over decadal scales (Smale, 2019; Drakard et al., 2023).

6.2 Implementation process of adaptation strategies and key technical measures

Adaptation in kelp farming generally begins with risk recognition, followed by adjustments in siting, seedstock, farm design, and seasonal operations. In China, proposed responses to climate pressure include preserving wild and cultivated germplasm, selecting sites suited to changing environmental conditions, breeding stress-resistant cultivars, and adopting innovative cultivation models. Similar ecosystem-based guidance from Europe and North America emphasizes climate resilience, protection of wild genetic diversity, and management systems that account for environmental carrying capacity (Hu et al., 2021).

Site selection is a first-line adaptation because local exposure strongly shapes farm vulnerability. Chinese reviews identify the selection of suitable cultivation sites under changing conditions, including possible expansion into more offshore spaces, as a major response to warming and other coastal pressures. Canadian case evidence similarly shows that adaptive management can favor cooler and more wave-exposed sites, while reducing harvests in warmer years and shifting harvest earlier when seasonal warming arrives unusually soon (Hu et al., 2021; Denley et al., 2025).

A second implementation pathway is biological improvement of farm stock. Recent experimental work suggests that thermal priming of *Saccharina latissima* gametophytes can increase subsequent sporophyte growth by up to 30% and extend tolerance under heat stress, indicating a practical crop enhancement route for warming seas. Genomic work on southern Chinese *S. japonica* cultivars further indicates that adaptation to relatively high seawater temperature involves changes in amino acid metabolism, sugar metabolism, osmotic regulation, and innate immune responses, supporting selective breeding for thermal resilience (Figure 2).

A third pathway is engineering adaptation. Because sheltered nearshore space is limited, offshore cultivation is increasingly proposed as a climate adaptation option, but it requires more robust infrastructure. Engineering analyses

show that offshore systems must withstand strong waves, currents, and wind, and that mooring-line cost is a dominant determinant of capital expenditure, so technical adaptation depends not only on biological feasibility but also on structural reliability and economic design (Hu et al., 2021; Lian et al., 2024).

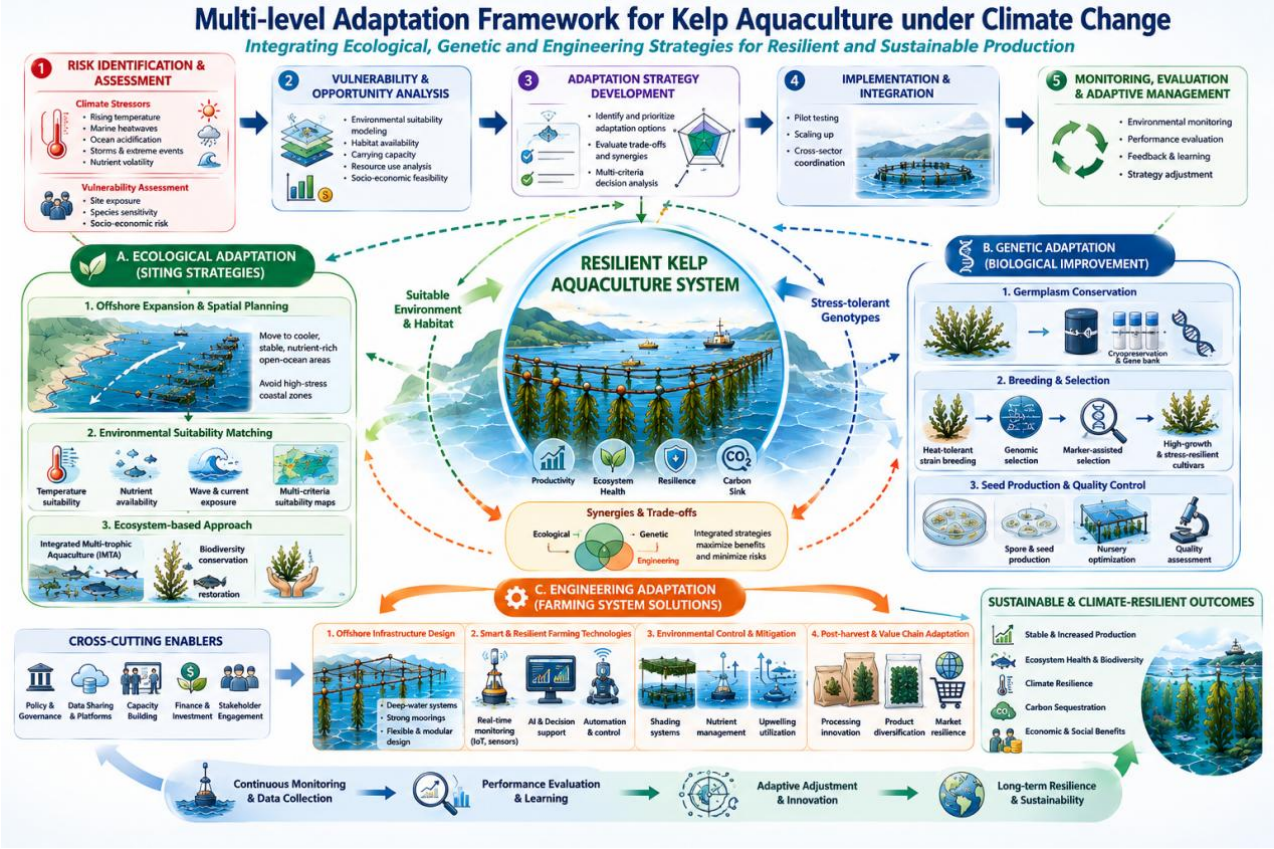

Figure 2 Multi-level adaptation framework for kelp aquaculture under climate change integrating ecological, genetic, and engineering-based strategies

6.3 Evaluation of ecological, economic, and social benefits

The ecological benefits of adaptation are strongest when strategies maintain production while also reducing environmental pressure in coastal waters. In China, kelp cultivation has already been estimated to remove substantial amounts of nitrogen and phosphate, assimilate large quantities of CO_2, and release oxygen, indicating that climate-resilient kelp farming can support nutrient management and carbon-related ecosystem services when farms remain productive. At broader scales, kelp systems generate major ecosystem-service value through fisheries support, nutrient cycling, and carbon removal (Hu et al., 2021).

These benefits, however, should not be overstated. Farm-scale evidence from Rhode Island found that a small sugar kelp farm produced negligible local ocean-acidification mitigation over a full growing season, with signals small relative to natural variability. Reviews of kelp farm biodiversity similarly conclude that farms can provide habitat and some ecosystem services, but they usually create novel communities rather than functioning as ecological equivalents of natural kelp forests (Forbes et al., 2022).

Economic gains from adaptation depend on both output stability and production efficiency. A life-cycle assessment of a 400-hectare Chinese kelp farm found relatively low climate impacts per ton of fresh kelp compared with smaller evaluated systems, while identifying plastics and buoys as key hotspots and recycling as the most effective improvement measure. In Europe, socioeconomic assessment from Sweden suggests that large-scale kelp farming can become profitable, but that biomass market value, rather than nutrient-removal payments alone, is likely to drive industry expansion (Hasselström et al., 2020; Li et al., 2023).

Social benefits are most evident where adaptation is embedded in local governance and livelihood systems. Maine's experience shows that kelp farming can diversify coastal economies and is often valued partly for ecological and ethical production practices, while broader ecosystem-approach work links the sector to alternative livelihoods and community well-being. On Canada's Pacific coast, co-designed monitoring with Indigenous stewardship organizations shows that adaptation can also strengthen social-ecological resilience by aligning harvest decisions with local knowledge, climate signals, and community priorities (Denley et al., 2025).

Across typical kelp farming regions, climate adaptation is most effective when it combines site selection, resilient seedstock, engineering upgrades, and participatory management. The evidence supports real ecological, economic, and social gains, but it also shows that benefits are context-dependent and strongest when claims remain aligned with measured outcomes.

7 Issues and Challenges in Climate Change Adaptation for Kelp Aquaculture

Climate change adaptation in kelp aquaculture is constrained not only by the direct effects of warming, acidification, storms, and disease, but also by uncertainty over how these stressors will interact across locations, species, and farming stages (Veenhof et al., 2024; Yadav et al., 2024). These uncertainties complicate decisions on site selection, breeding priorities, farm design, harvest timing, and investment planning, especially in emerging farming regions where long-term operational experience remains limited (Coleman et al., 2022; Veenhof et al., 2024).

At the same time, adaptation is not simply a technical problem. Its success depends on whether farmers can access affordable technologies, whether new systems are economically viable at commercial scale, and whether governance frameworks are flexible enough to support forward-looking responses rather than reactive coping. For kelp aquaculture, the major challenges therefore lie in managing climate uncertainty, overcoming technological and financial barriers, and building policy systems that can enable planned adaptation over long time horizons (Veenhof et al., 2024).

7.1 Risks associated with climate change uncertainties

A central challenge for kelp farming is that future climate exposure is difficult to predict with sufficient local precision for operational decisions. Ocean warming, acidification, altered seasonality, and extreme events can reduce kelp biomass, shift biochemical composition, and damage farms, but their intensity and timing vary across regions and years (Veenhof et al., 2024). More broadly, aquaculture adaptation depends on projections that are accurate enough to guide producers, because unrealistic or biased estimates of climate risk can mislead both farmers and policymakers and increase the risk of maladaptation (Maulu et al., 2021).

Uncertainty is amplified because multiple stressors often act together, while the evidence base remains uneven across stressor types and life stages. High-latitude kelps are projected to face range contractions, with risks intensified by marine heatwaves and increased freshwater and sediment inputs, yet important gaps remain in understanding how kelp microstages respond to combined stressors (Drakard et al., 2023). Risk assessments also suggest that future warming may make seaweed farming unviable in some current production regions, which means adaptation planning must account for the possibility that incremental adjustments will not always be enough (Kim et al., 2024).

7.2 Limitations regarding the adoption of adaptation technologies and investment costs

Although adaptation options such as selective breeding, diversification, improved nursery systems, and offshore expansion are widely discussed, their adoption is limited by technical complexity and cost. Reviews of climate-resilient aquaculture identify selective breeding, species diversification, and advanced systems as leading adaptation pathways, but more complex solutions generally require greater expertise and become less accessible as costs rise (Yadav et al., 2024). This constraint is especially relevant for kelp farming because resilience strategies often depend on research-intensive interventions such as breeding for tolerance, microbiome manipulation, or engineering systems suited to exposed environments (Veenhof et al., 2024).

Economic barriers also extend beyond farm hardware to the full production chain. Techno-economic modeling of kelp nurseries shows that reducing grow-out duration, increasing labor capacity, and de-risking energy-efficient systems are key priorities for lowering costs, while wider industry analyses point to operational optimization, weak supply chains, market uncertainty, and difficulty achieving economically viable scale as persistent obstacles (Coleman et al., 2022; Canvin et al., 2025). Even when seaweed farming is sometimes described as low-investment in principle, expansion into new regions or more climate-resilient production models often requires substantial infrastructure, financing, logistics, and external support that many small or early-stage producers do not have (Canvin et al., 2025).

7.3 Insufficiencies in policy support and management system development

Policy and management systems have generally not kept pace with the adaptation needs of aquaculture. National climate adaptation strategies often acknowledge climate risks broadly but seldom include aquaculture-specific measures, even though aquaculture needs to be integrated into national and regional adaptation plans to avoid being disadvantaged by policies designed for other sectors. For kelp farming, this gap is particularly important because farm siting, environmental monitoring, biosecurity, and licensing all require governance systems that can respond to changing climatic conditions rather than assuming static baselines.

Existing governance frameworks also tend to be fragmented, rigid, and overly reactive. Legal analysis of marine aquaculture adaptation in Chile found poor implementation of committed measures, lack of strategic vision, and planning and leasing systems too inflexible to support effective adaptation. Similar concerns appear in broader seaweed policy debates, where regulatory complexity, exclusion from carbon-accounting frameworks, and the need for standardized valuation and long-term conservation strategies continue to slow investment and coordinated management development (Chandrani et al., 2024; Canvin et al., 2025).

8 Conclusions and Future Outlook

Kelp aquaculture is likely to remain a strategically important component of climate-resilient marine food systems, but its future will depend on whether adaptation keeps pace with increasingly complex environmental change. Across the literature, the dominant message is that warming, altered seasonality, extreme events, and biological stressors are already reshaping cultivation risks, while the sector still retains strong potential to support food production, ecosystem services, and broader sustainability goals. Current evidence shows that climate change affects kelp aquaculture through multiple interacting pathways rather than through warming alone. A recent global meta-analysis found that ocean warming has strong negative effects on kelps across growth, reproduction, and survival, while acidification alone is generally weaker but can still impair reproduction; experimental work on bull kelp similarly shows that higher temperature reduces gametophyte survival and offspring production, even when lower pH has less negative effects on some early stages.

From an industry perspective, these physiological responses translate into operational risks such as lower biomass yield, altered biochemical composition, greater disease vulnerability, and damage from marine heatwaves, storms, and freshwater inputs. Reviews focused on North Atlantic seaweed aquaculture identify abiotic change, extreme events, and disease as major climate-related threats, while broader aquaculture syntheses show that harmful algal blooms, salinity change, and shifting ecological dynamics further complicate farm management and sustainability planning. The effects of climate change are also uneven across regions and species, which means exposure cannot be generalized from one farming area to another. Species farmed near their upper thermal limits are expected to be most vulnerable, whereas some colder regions may temporarily gain suitability as temperature or ice constraints relax; similarly, assessments of marine aquaculture potential project heterogeneous geographic gains and losses but an overall greater probability of declines under continued warming.

A comprehensive understanding therefore requires integrating farm biology with local oceanography, infrastructure limits, and socioeconomic context. Resilience studies in coastal farming communities show that climate impacts do not act on production alone but also on livelihoods, adaptive capacity, and equity, reinforcing the need to frame kelp aquaculture as a social-ecological system rather than only a biological crop system. The most consistently supported

adaptation strategies are future-proof site selection, selective breeding or trait selection, ecosystem-based farm design, and stronger environmental monitoring. Reviews of North Atlantic seaweed aquaculture identify site selection, breeding and microbiome manipulation, and restorative aquaculture as the three main resilience pathways, while general climate-resilient aquaculture reviews similarly emphasize selective breeding, diversification, ecosystem-based management, and advanced systems as core adaptation tools.

These strategies appear effective when matched to the dominant local stressors, but evidence for each remains uneven. Site selection is strengthened by improved oceanographic and climate modelling, and biotechnology-oriented approaches such as tissue culture, selective breeding, and genetic engineering show promise for improving stress tolerance and yield; however, many of these interventions are still developing, and their commercial performance under open-water farming conditions is not yet fully resolved. Some adaptation benefits are already measurable at farm scale. Seaweed farms can buffer local acidification, with *Saccharina japonica* farms showing mean pH increases of about 0.10 and reduced pCO_2 relative to surrounding waters, which supports the view that farming can create localized refugia from acidification and deoxygenation.

Even so, adaptation effectiveness should not be judged only by whether kelp survives climate stress. Large-scale farming can introduce trade-offs such as habitat disruption, nutrient competition, or uncertain carbon benefits, so strategies are most credible when paired with habitat-friendly practices, IMTA, and rigorous monitoring and regulation rather than treated as universally beneficial solutions. Future development should prioritize breeding and seed systems, predictive farm planning, and cultivation technologies that are robust under a warmer and more variable ocean. The literature points to opportunities in omics-assisted breeding, targeted microbe treatments, and wider use of resilient species or strains, while also highlighting offshore farming and advanced monitoring as promising directions for sustaining production under climate stress. At the same time, the next phase of industry development will require stronger supporting systems beyond farm technology alone. Reviews from Norway and Tanzania both show that climate resilience depends on adapted regulatory frameworks, coordinated support, farmer training, and investment in improved varieties and knowledge transfer, especially where producers have limited capacity to absorb climate shocks on their own.

Another major priority is to build credible frameworks for environmental accounting and risk governance. Seaweed carbon accounting remains poorly developed, and robust monitoring, reporting, and verification systems are still needed to quantify sequestration pathways, evaluate trade-offs, and distinguish realistic climate services from claims that outpace the science. In the longer term, a climate-resilient seaweed industry will likely emerge from cross-sector integration rather than from farm expansion alone. Recent syntheses call for stronger global research collaboration, integration of new technologies, and development of robust value chains and circular bioeconomy pathways so that seaweed farming can support food security, low-carbon materials, and sustainable coastal livelihoods under climate change. Kelp farming under climate change is therefore best understood as a conditional opportunity: the sector shows real adaptive potential, but durable success depends on combining biological innovation, careful siting, ecological safeguards, and supportive institutions. Future progress will be strongest where resilience is pursued as a system-level strategy, not as a single technical fix.

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