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International Journal of Marine Science, 2026, Vol. 16, No. 1, 55-65

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Effects of Different Feeding Strategies on the Production Performance of Pacific White Shrimp

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Abstract Pacific white shrimp (*Litopenaeus vannamei*) is one of the most economically important aquaculture species worldwide, and feed management plays a crucial role in determining production efficiency and profitability. Different feeding strategies can significantly influence shrimp growth performance, feed utilization, water quality, and overall economic returns. This paper reviews the nutritional requirements and feeding characteristics of Pacific white shrimp and systematically evaluates the effects of various feeding strategies, including fixed-time and fixed-quantity feeding, multiple small-meal feeding, and intelligent precision feeding. The impacts of these strategies on growth rate, survival rate, feed conversion ratio, environmental conditions, and disease management are analyzed. In addition, their economic implications, such as feed costs, production efficiency, and return on investment, are discussed. A comparative case study is presented to illustrate the practical performance of different feeding approaches in commercial shrimp farming systems. The findings indicate that optimized feeding management can improve feed utilization efficiency, enhance shrimp health, reduce environmental impacts, and increase farm profitability. Furthermore, the integration of intelligent feeding technologies offers promising opportunities for sustainable and precision aquaculture. This review provides valuable insights for researchers, aquaculture practitioners, and policymakers seeking to improve the productivity and sustainability of Pacific white shrimp farming.

Keywords Pacific white shrimp; Feeding strategy; Feed utilization efficiency; Aquaculture economics; Precision feeding technology

1 Introduction

The Pacific white shrimp *Litopenaeus vannamei* has become the dominant farmed crustacean worldwide and a cornerstone of the global seafood market, contributing a large share of aquaculture production and animal protein supply. Its commercial success is driven by fast growth, high survival, and tolerance to a wide range of environmental conditions and high stocking densities, making it attractive for intensive and super-intensive systems in both coastal and inland areas (Qiao et al., 2023). At the farm level, intensive pond and tank operations routinely achieve several thousand kilograms per hectare per cycle with favorable financial indicators, highlighting the strong economic potential of this industry when production is efficiently managed (Farkan et al., 2024).

Despite these advantages, the sustainability and profitability of *L. vannamei* culture are tightly constrained by feed costs and feeding efficiency. Feed typically accounts for more than half of the operating or variable costs in shrimp farming, and in some cases approaches 60%-68% of total variable expenses. Surveys of commercial farms similarly show that large feed inputs and resulting feed conversion ratios are key determinants of economic performance, with higher FCRs negatively affecting farm profitability. Beyond economics, excessive feed inputs are a primary source of nutrient loading, deteriorating water quality and generating nitrogen and phosphorus-rich effluents that accumulate in pond water and sediments, increasing environmental risks and reducing long-term sustainability. Consequently, optimizing feed use is central not only to reducing production costs, but also to improving ecological performance and resource efficiency in intensive shrimp aquaculture (Chaikaew et al., 2019; Da Silva et al., 2023).

Within this context, feeding strategy—encompassing ration level, feeding frequency, delivery method, and integration with natural food or biofloc—has emerged as a critical lever for improving production performance of Pacific white shrimp. Evidence from pond and tank trials under semi-intensive and intensive conditions shows that modifying feed amounts, frequencies, or the use of automatic and demand-feeding systems can significantly alter

growth, final weight, and economic returns without necessarily compromising survival or FCR. In biofloc and integrated multi-trophic systems, reduced feeding rates or minimum table-based rations have been shown to maintain acceptable growth while markedly improving FCR and lowering feed costs, indicating that natural productivity and microbial flocs can partially substitute formulated feed when feeding regimes are carefully adjusted (Gonçalves et al., 2024). Other studies emphasize the importance of aligning feeding rates and frequencies with shrimp behavior and physiology, demonstrating that strategies such as more frequent small meals, optimal feeding frequencies with automatic feeders, or moderate feed restrictions can enhance growth, feed utilization, antioxidant capacity, and profitability, while avoiding overfeeding and unnecessary nutrient loading.

Nevertheless, despite growing recognition that feeding management strongly shapes growth, feed efficiency, environmental footprint, and economic outcomes, information on optimal feeding strategies for Pacific white shrimp across different culture systems and intensities remains incomplete, especially under commercial-scale conditions. There is a clear need to systematically evaluate how different feeding strategies influence production performance—such as growth rate, survival, FCR, and economic returns—under realistic farming scenarios, including ponds, recirculating systems, and biofloc-based operations. The present study, titled “Effects of Different Feeding Strategies on the Production Performance of Pacific White Shrimp,” aims to address this gap by comparing alternative feeding regimes designed to adjust ration level and feeding pattern, and by quantifying their impacts on growth performance, feed utilization, and production economics. By identifying feeding strategies that balance high productivity with reduced feed inputs and environmental loading, this research seeks to provide practical guidance for farmers to enhance profitability and sustainability in Pacific white shrimp aquaculture.

2 Nutritional Requirements and Feeding Characteristics of Pacific White Shrimp

2.1 Nutritional requirements at different growth stages of pacific white shrimp

Protein is a primary driver of growth in Pacific white shrimp, but the optimal level shifts with body size and developmental stage. Feeding trials across juvenile, sub-adult, and adult stages indicate that crude protein requirements for maximum growth generally fall around 32%-36%, with slightly higher levels for smaller shrimp and modest reductions as shrimp grow larger. In larvae, diets containing about 35% protein have produced superior weight gain and protein efficiency, suggesting that early life stages also benefit from moderately high but not excessive protein inputs (Elfeky, 2022).

Energy supply through lipids must be balanced with protein so that protein is used for growth rather than as an energy source. Studies combining different protein and lipid levels in juvenile shrimp identify an optimal protein-energy ratio around 340 g/kg protein with moderate lipid (about 75 g/kg), which maximizes growth, protein efficiency, and feed efficiency without excessive fat deposition. For postlarval shrimp, graded lipid trials suggest an optimal dietary lipid level near 118-124 g/kg when both growth and stress tolerance are considered, highlighting that very young stages may tolerate or require higher lipid levels to support rapid growth and resilience (Xie et al., 2019).

2.2 Feeding behavior and influencing factors

Feeding behavior in Pacific white shrimp is strongly shaped by environmental conditions, especially temperature. Experimental work shows that at cooler temperatures (around 24 °C-28 °C), juveniles feed slowly on the tank bottom, with long gut-filling and evacuation times and substantial uneaten feed remaining after meals. As temperature rises to 30 °C-34 °C, shrimp swim actively while feeding, fill their guts within 15-20 minutes, and consume nearly all the offered pellets, indicating a sharp temperature-dependent acceleration of intake and digestion. Parallel growth trials confirm that growth rate and feeding rate increase with temperature, but the optimal temperature for fastest growth declines as shrimp size increases, implying that feeding strategies should be adjusted to both size and thermal regime.

Beyond temperature, social and environmental context also modifies feeding behavior and efficiency (Figure 1). Behavioural studies show that stocking density and dominance hierarchies affect how long individuals spend on the feeding area and how feed is partitioned; at higher densities, shrimp show greater relative feed consumption but

share limited feeding space, while dominance-related differences in feeding time are reduced (Bardera et al., 2021). Turbidity alters group-level responses, with higher turbidity increasing feed intake and reducing distances between individuals, suggesting that commercial ponds with naturally turbid conditions may promote more cohesive and intense feeding bouts than clear-water tanks (De Tailly et al., 2025).

Mechanistic diagram of the effects of temperature gradient on the feeding behavior of *Litopenaeus vannamei*

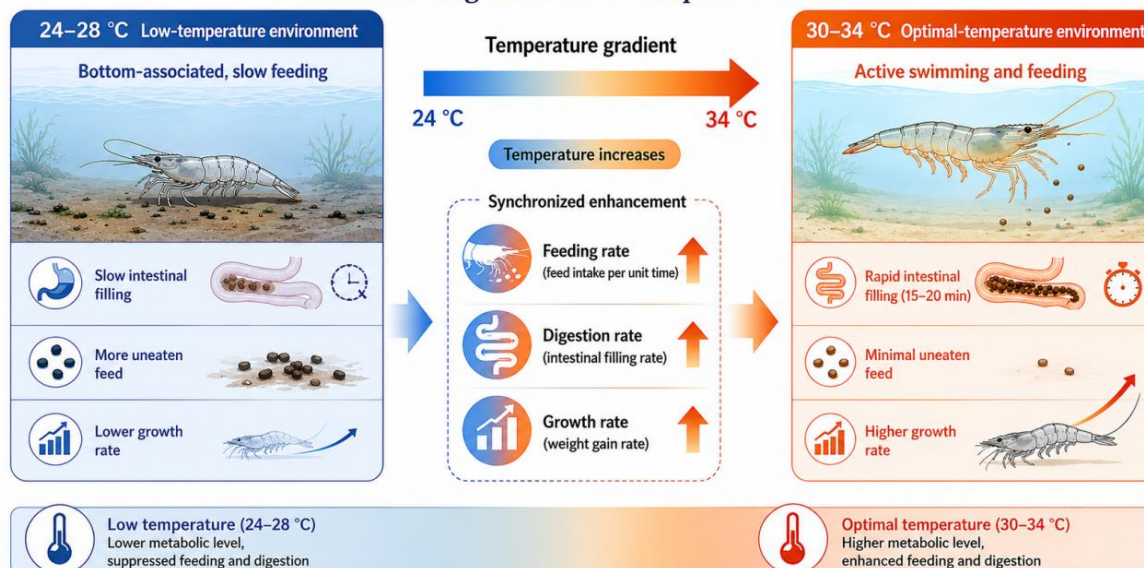


Figure 1 Effects of water temperature on feeding behavior, digestive activity, and growth performance of Pacific white shrimp (*Litopenaeus vannamei*)

Note: Shrimp reared at 24 °C-28 °C exhibit slower feeding activity, prolonged gut-filling and evacuation times, and increased feed residues, whereas individuals maintained at 30 °C-34 °C show rapid feed consumption, accelerated digestion, and enhanced growth

2.3 Relationship between feed utilization efficiency and growth performance

Feed utilization efficiency, commonly expressed as feed conversion ratio (FCR), is tightly linked to growth performance and is influenced by diet formulation and feeding rate. In intensive systems, increasing feeding rates above a standard schedule leads to higher final weights, but FCR worsens and growth approaches a plateau, revealing an inflection point near 100%-101% of the standard feeding rate where additional feed yields diminishing returns. Trials manipulating feeding frequency in juveniles similarly show that moderate automatic feeding (around 6-8 meals per day) improves FCR, final weight, and antioxidant status compared with less frequent manual feeding, indicating that spreading the same ration into more meals can enhance nutrient utilization (Liang et al., 2025).

Dietary interventions that improve digestion or metabolic efficiency can reduce FCR while supporting growth. Supplementation of low-fishmeal, low-lipid diets with small amounts of lysophospholipids increases final body mass, growth rate, and protein deposition, while lowering FCR and enhancing digestive enzyme activities and intestinal health, demonstrating how additives can “unlock” feed efficiency under cost-saving formulations (Li et al., 2026). Similarly, nanoemulsified curcumin in olive oil has been shown to improve specific growth rate, FCR, and protein efficiency ratio, alongside better digestive enzyme secretion and antioxidant capacity, linking enhanced physiological status to more efficient feed use (El-Bab et al., 2024).

3 Common Feeding Strategies and Their Characteristics

3.1 Fixed-time and fixed-quantity feeding strategy

In many commercial farms, shrimp are fed at fixed times and fixed daily rations based on biomass estimates or standard feeding tables. This approach is simple to implement and relies on scheduled distributions (for example, two to four meals per day) with predetermined quantities that are adjusted periodically as shrimp grow. Semi-intensive pond trials using standard feeding protocols (SFP) show that applying a fixed ration close to a

reference curve can support good growth and survival under both tank and pond conditions. In these studies, reducing or increasing feed input around the SFP (for example, 90%-110% of the table) had limited effect on feed conversion ratio, suggesting that fixed-ration strategies can be robust when biomass estimates are reasonable (Van et al., 2017).

However, strictly fixed rations may fail to match real-time appetite, especially as natural food availability and environmental conditions fluctuate. In intensive biofloc systems, experiments that applied several discrete feeding levels (30%-150% of a standard rate) revealed that growth increases with higher feed inputs but feed conversion worsens once a threshold is exceeded, indicating a trade-off between maximum biomass gain and feed efficiency under fixed-rate feeding. These results highlight that while fixed-time and fixed-quantity strategies are practical, they require careful calibration to avoid underfeeding, which limits growth, or overfeeding, which raises costs and nutrient loading (Weldon et al., 2021).

3.2 Multiple small-meal feeding strategy

Shrimp have small stomachs and naturally ingest many small meals, so distributing the daily ration into multiple small feedings aims to better align with their feeding behavior. Controlled studies comparing low (1-2 meals) and higher frequencies (4-6 meals or more) show that more frequent feeding can improve growth and, in some cases, water quality when total ration is maintained. For example, juveniles in biofloc systems fed three, six, or twelve times daily with the same daily ration displayed higher final weight, yield, and protein deposition as frequency increased, while feed conversion ratio decreased (Xu et al., 2020). Similar trials with extruded diets found that once- or twice-daily daylight feeding promoted growth but at the expense of water quality and FCR, whereas higher frequencies reduced ammonia and nitrite levels, indicating environmental benefits of spreading meals (Espinoza-Ortega et al., 2023).

Multiple small-meal strategies can be implemented manually or via automatic feeders and may be particularly valuable when diet formulation or system design constrains performance. Using a low-fish-meal, amino-acid-supplemented diet, offering ten meals per day via automatic feeders enhanced survival, body weight, and FCR compared with two or four manual meals, illustrating that more frequent feeding can compensate for lower fish-meal inclusion by improving intake and nutrient use. On farms, observations of pond management practices similarly emphasize dividing rations into several daily feedings and monitoring consumption, supporting more even distribution and reducing cannibalism, which are key practical characteristics of multiple small-meal feeding (Andriani and Pratama, 2023).

3.3 Intelligent precision feeding strategy

Intelligent precision feeding integrates automatic devices and real-time feedback or predictive models to dynamically adjust feed delivery according to shrimp demand and biomass. On-demand acoustic systems such as AQ1 release feed in response to feeding sounds, allowing shrimp to “request” feed within programmed limits. Pond trials comparing acoustic demand feeding with fixed-schedule timer feeders and standard protocols demonstrate that AQ1 systems consistently produce larger shrimp, higher yields, and greater crop value, without worsening FCR or survival, indicating more precise matching of feed input to appetite. Follow-up work under semi-intensive conditions similarly found that automatic feedback systems operating in real time outperformed standardized timer-based schedules, reinforcing the performance advantage of demand-driven feeding (Reis et al., 2020).

Beyond behavior-based feedback, recent developments incorporate machine-learning biomass prediction into intelligent feeders. In recirculating systems, data-driven models using water-quality and management data can predict shrimp biomass with high accuracy, enabling feeders to calculate appropriate ration sizes and stabilize water quality. Automated feeding trials that varied the number and distribution of meals show that when combined with optimized schedules, these systems improve growth and FCR compared to manual feeding, while also reducing labor costs and enabling higher feeding frequencies (Liang et al., 2025). Overall, intelligent precision strategies are characterized by continuous or high-frequency feed delivery, sensor or acoustic feedback, and algorithm-guided ration adjustment, aiming to maximize growth and profitability while minimizing waste.

4 Effects of Different Feeding Strategies on the Growth Performance of Pacific White Shrimp

4.1 Effects on weight gain and specific growth rate

Feeding rate and rationing strategy have clear impacts on weight gain and specific growth rate (SGR) of Pacific white shrimp. In high-density biofloc systems, increasing feeding rates above a reduced baseline progressively increased final weight and weekly growth, but gains tended to plateau as rates exceeded the level needed to approach maximum growth. Similarly, in biofloc grow-out systems, a moderate 25% reduction in feeding rate unexpectedly produced the highest final weight, biomass, and weight gain, indicating that natural food sources can compensate for reduced formulated feed while still supporting rapid growth and high SGR (Kusmiatun et al., 2025).

Feeding frequency and delivery method also shape weight gain and SGR, even when the total daily ration is similar. In ponds, increasing daily feedings from two to six times using timer or acoustic demand systems significantly raised final individual weights compared with twice-daily protocols, showing that distributing feed more evenly enhances growth performance. Recirculating tank trials with automatic feeders further highlight that feeding 6-8 times per day optimizes final body weight and SGR compared with both lower-frequency manual feeding and higher-frequency automatic schedules, suggesting that there is an optimal feeding frequency window beyond which additional meals do not improve, and may even impair, growth (Liang et al., 2025) (Figure 2).

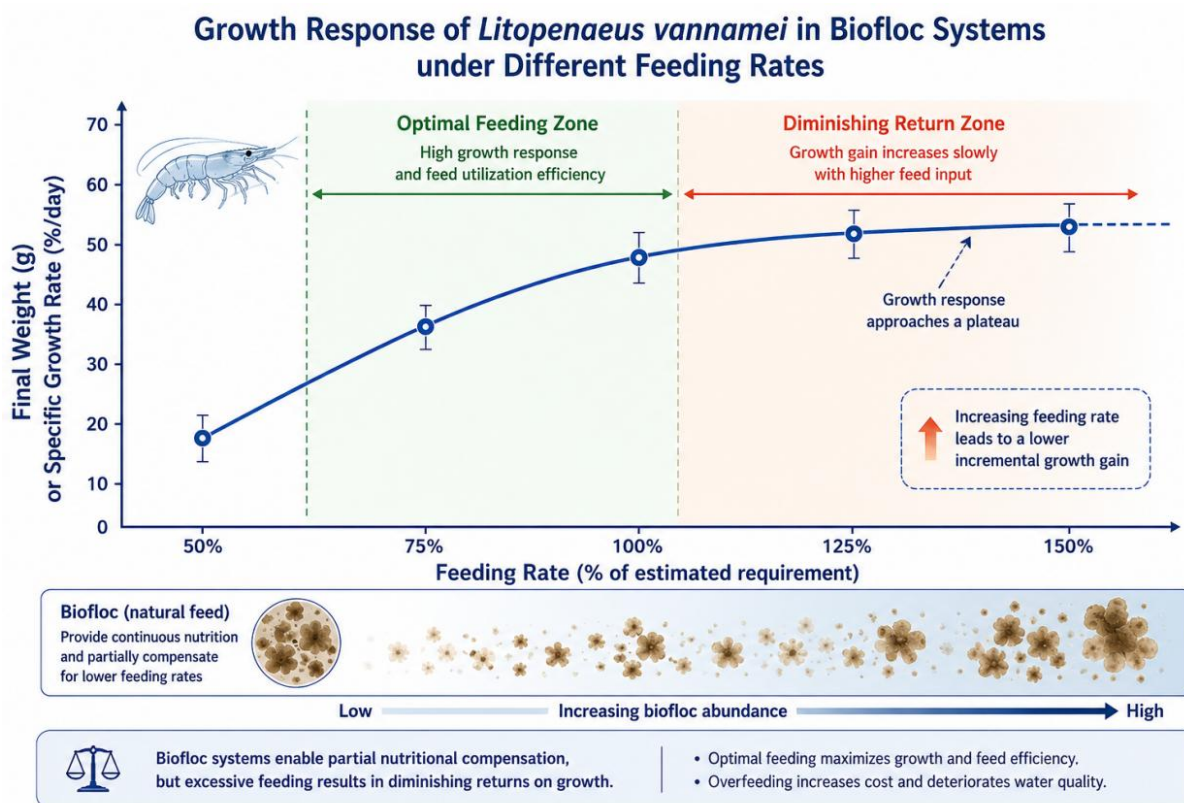


Figure 2 Conceptual relationship between feeding rate and growth performance of Pacific white shrimp (*Litopenaeus vannamei*) cultured in biofloc systems

4.2 Effects on survival rate and culture duration

Many feeding strategies that alter ration level or delivery pattern can maintain high survival while modifying growth trajectories, which has implications for culture duration. In intensive biofloc systems exposed to a wide range of feeding rates, survival remained consistently high (around 94%-97%) across treatments, indicating that shrimp tolerate substantial variation in feed inputs over a 63-day cycle without major mortality effects. Nursery-phase biofloc studies similarly reported no significant differences in survival or feed conversion ratio when feeding frequency was reduced from six to one meal per day over 40 days, suggesting that survival in early nursery stages is relatively robust to feeding frequency adjustments under good water quality (Wasielesky et al., 2020).

Under integrated multi-trophic systems, survival outcomes can even improve under adjusted feeding regimes. In tanks co-culturing shrimp with the macroalga *Caulerpa lentillifera*, survival and yield at 75%-100% of the control feed ration were significantly higher than in monoculture controls over 45 days, despite reduced formulated feed inputs. Biofloc-based studies cutting feed by 25% also maintained good survival while shortening effective time to marketable size through higher SGR, implying that optimized feed reductions in enriched systems may sustain or improve survival while potentially reducing culture duration required to reach target weights (Kusmiatun et al., 2025).

4.3 Effects on size uniformity within shrimp populations

Feeding strategies influence how evenly feed is distributed among individuals, thereby affecting size uniformity. Experiments manipulating pellet (diet) size showed that larger pellets prompted more aggressive feeding behavior, with some shrimp obstructing others and monopolizing feed; this “selfish” behavior was suggested as a mechanism leading to considerable size variation and potentially higher mortality among smaller individuals as they grow to market size. Practical feeding recommendations from field observations similarly stress that even feed distribution in ponds is essential to promote proportional growth, indicating that unequal spatial delivery of feed can exacerbate within-cohort size differences (Andriani and Pratama, 2023).

Feeding frequency and access time also interact with social dynamics to influence size dispersion. Studies of stocking density and dominance in *L. vannamei* showed that density and social rank affect time spent feeding, with dominant individuals securing more feeding opportunities under certain conditions. Automatic or demand-based feeding systems that provide more continuous access to feed throughout the day can partially mitigate competitive exclusion by extending feeding windows, which likely contributes to the improved growth observed with acoustic demand feeders compared with limited twice-daily hand feeding in ponds (Ullman et al., 2018).

5 Effects of Different Feeding Strategies on Feed Utilization Efficiency

5.1 Effects on feed conversion ratio (FCR)

Feed conversion ratio is highly sensitive to how much and how often shrimp are fed, with both restrictive and excessive rations altering efficiency. In high-density biofloc systems, varying feed inputs from 30% to 150% of a standard rate showed that increasing feed above about 100% raised final weight but caused FCR to increase, indicating diminishing returns in growth relative to feed supplied. Regression analysis also identified an inflection near 101% of the standard rate where feed utilization declined rapidly, emphasizing that overfeeding directly worsens FCR even when growth continues to rise (Weldon et al., 2021).

Feed restriction and the use of natural productivity can conversely improve FCR when carefully managed. In a synbiotic pond system, partial feed restriction reduced FCR from 0.59 under full feeding to 0.30 under restricted feeding while still allowing total compensatory growth, showing that lower rations can markedly increase efficiency if environmental food is available. Similarly, in biofloc tanks, a 25%-50% reduction in feeding rate produced the lowest FCR values (0.90-0.71) compared with standard rations in clear water or biofloc, illustrating that biofloc-based strategies can substantially enhance FCR under reduced feed inputs (Kusmiatun et al., 2025).

5.2 Effects on dietary protein utilization efficiency

Feeding strategies that alter protein intake and ration size strongly affect protein retention and utilization. In a green-water recirculating system, combinations of 25%-40% dietary protein and two feeding rates produced significant differences in apparent net protein retention (49%-66%), with lower protein intake treatments achieving the highest retention despite slower growth (Araujo et al., 2025). This indicates that high feeding and protein levels favor growth but can dilute protein efficiency, whereas more modest protein supplies improve retention per unit intake.

Biofloc-based feeding reductions can simultaneously improve growth and protein utilization when natural food supplements the diet. In a 30-day biofloc trial, a 25% feed reduction produced the highest final protein content and protein retention (18.94%) compared with standard feeding in clear water or biofloc, demonstrating more effective

conversion of ingested protein into body tissue under moderate restriction (Kusmiatun et al., 2025). Cyclical fasting-feeding regimes also improved protein efficiency ratio in juveniles, suggesting that intermittent restriction can enhance protein use while maintaining compensatory growth.

5.3 Effects on production efficiency and resource use

At the farm scale, FCR is closely tied to economic and environmental performance, so feeding strategies that lower FCR directly improve resource use. Nutrient-budget analysis on an intensive farm showed that feed contributed 80% of nitrogen inputs, with an overall FCR of 2.0; modeling a reduction to 1.8 FCR indicated the farm could cut 147 kg of feed, saving over US\$1000 per crop and reducing nitrogen and phosphorus loading to ponds and effluents. Global assessments of embodied resources in shrimp feeds further suggest that reducing FCR by 0.1 across major cultured species would save large amounts of energy, land, freshwater, and wild fish, underscoring the broader sustainability gains from efficient feeding.

Within biofloc and synbiotic systems, feed-restriction strategies can maintain or even improve production efficiency while lowering operational inputs. In synbiotic ponds, partial feed restriction halved FCR and reduced total operating costs by about 20%, yet both restricted and unrestricted treatments showed positive profitability, indicating that lower feed input strategies can be economically viable (Gonçalves et al., 2024). Complementary work in biofloc systems found that feeding according to minimum table values yielded better FCR, survival, and lower waste production than maximum table rates or FCR-based rationing, highlighting that conservative, well-calibrated feeding tables can improve both resource use and system cleanliness (Da Silva et al., 2023).

6 Effects of Different Feeding Strategies on Culture Environment and Health Management

6.1 Effects on water quality parameters

Feeding rate and delivery method directly affect nutrient loading and key water quality variables in shrimp culture systems. In semi-intensive ponds, increasing feed inputs raised nitrogen and phosphorus concentrations, elevating total ammonia nitrogen and nitrite, particularly when demand feeders allowed higher daily feed loads than hand feeding or timer-based protocols. In indoor recirculating systems, sharp increases in feed load led to spikes in total ammonia nitrogen up to 24.2 mg/L, coupled with oxygen depletion and large mortality events, underscoring how overfeeding can overwhelm biofiltration capacity and destabilize water quality (Mohammed et al., 2024).

Feeding strategy can also modify suspended solids and organic matter dynamics in pond water. Comparisons between ponds using feeding trays and mechanical feed blowers showed that tray feeding generated lower ammonia and particulate organic solids loads per kilogram of shrimp, even though total suspended solids were slightly higher, suggesting tighter control of uneaten feed. In biofloc and zero-exchange systems, adjusting feeding levels interacts with microbial floc to influence ammonia; for example, nursery tanks with lower feeding rates showed significantly reduced ammonia compared with higher-fed controls, reflecting the role of feed load management in maintaining acceptable nitrogen levels (Khanjani et al., 2016).

6.2 Effects on pond sediment conditions and organic loading

Uneaten feed and feces are major contributors to sediment organic loading, and their accumulation is closely linked to feed management intensity. Field analysis of different shrimp culture intensities showed that estimated organic waste (total suspended solids) derived from feed rose from about 488 kg TSS/ha in traditional plus systems to over 9,228 kg TSS/ha in intensive ponds, reflecting higher feed use at greater stocking densities (Mhr, 2022). Nitrogen budget studies in penaeid ponds, although not specific to *L. vannamei*, similarly indicate that up to 38.4% of nitrogen entering as feed and inflow may accumulate in sediments, with waste generation per kilogram of shrimp increasing strongly with stocking density and associated feed inputs.

Sedimentation rates of nutrients and particulates also respond to management history and feed loading intensity. In *L. vannamei* earthen ponds, treatments associated with higher initial inputs for dense greenhouse phases showed significantly elevated early sedimentation of nutrients and particulate matter, indicating rapid deposition of feed-derived solids. In polyculture ponds with tilapia and shrimp, ponds classified as high feed-loading exhibited

sediment accumulation rates around 35.5 cm/year and markedly higher carbon burial than low-loading ponds, suggesting that persistent overfeeding accelerates pond infilling and long-term organic enrichment of sediments (Kunlapapuk et al., 2019).

6.3 Effects on disease risk and immune status

Feeding strategies interact with health management by shaping both environmental stressors and the nutritional support for immunity. Excess feed inputs elevate ammonia and nitrite, which can compromise shrimp condition and increase susceptibility to disease; high TAN associated with an 81.2% increase in feed load was linked with 40% mortality in a recirculating system, demonstrating how feed mismanagement can directly trigger health crises (Mohammed et al., 2024). Broader analyses of shrimp aquaculture wastewater identify excess feeding as a major source of organic and nutrient pollution, and recommend careful feed control as part of preventive health and environmental management to avoid eutrophication and related disease risks (Iber and Kasan, 2021).

Conversely, diet composition and functional feed additives within a given feeding strategy can enhance immune status and disease resistance. Probiotic-supplemented diets, such as those containing *Lactobacillus plantarum* Ep-M17 or *Pediococcus acidilactici*, improved growth, lowered feed conversion ratio, and significantly reduced mortality after *Vibrio parahaemolyticus* or *Fusarium solani* challenges, reflecting strengthened immune and antioxidant responses under routine feeding schedules. Similarly, herbal or functional additives such as artemisinin and lysozyme-based supplements enhanced antioxidant capacity, immune enzyme activities, and resistance to *Vibrio* infections, indicating that appropriately formulated and scheduled feeding can be a key tool in integrated health management strategies (Figure 3).

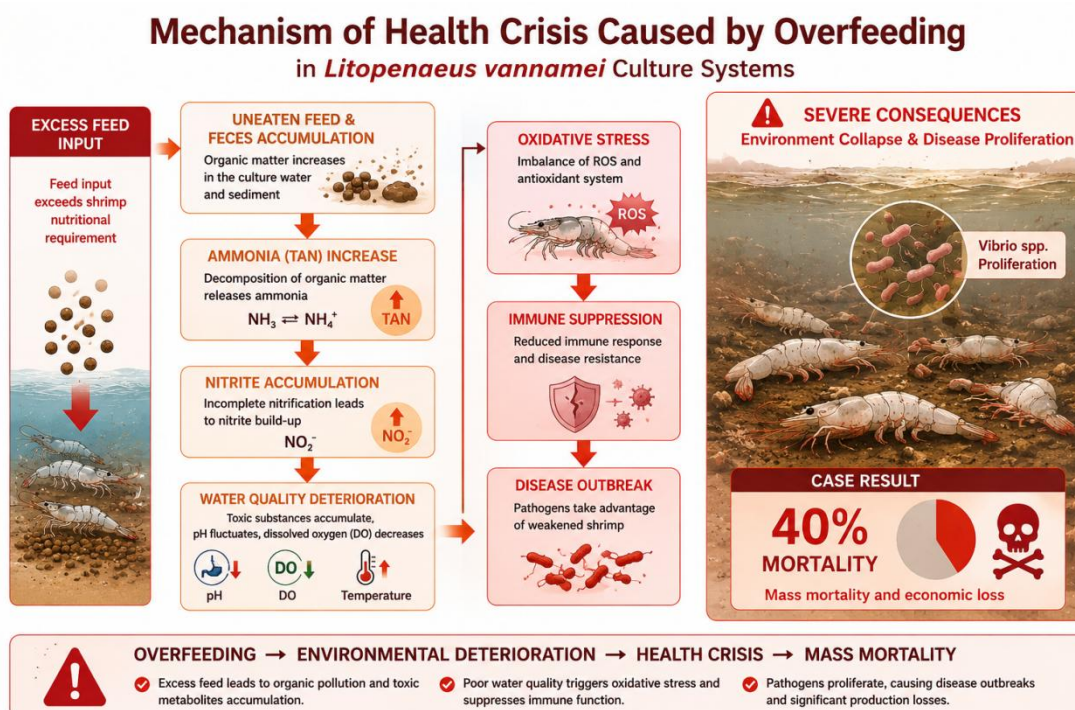


Figure 3 Mechanistic pathway linking excessive feeding to environmental deterioration and disease risk in Pacific white shrimp (*Litopenaeus vannamei*)

7 Effects of Different Feeding Strategies on Economic Benefits of Shrimp Farming

7.1 Analysis of feed costs and production costs

Feed is consistently identified as the largest component of variable production costs in Pacific white shrimp culture, so feeding strategy directly shapes overall cost structure. In Indian farms, feed accounted for about 69% of total variable costs, greatly exceeding other inputs such as seed, energy, and labor, which together represented less than one-third of variable expenditure. Similar analyses comparing *L. vannamei* and *P. monodon* across intensification

levels in India showed that feed alone represented about 70% of variable costs in whiteleg shrimp farms, underlining that small changes in feed use or price translate into large changes in total production cost per hectare (Nisar et al., 2021).

Because feed is such a dominant cost, strategies that reduce ration without harming growth can markedly lower total and operating costs. In a synbiotic pond system, partial feed restriction cut FCR by roughly half and reduced effective operating costs by 21.8% and total operating costs by 20.2%, with feed volume being the only cost component differing between treatments (Gonçalves et al., 2024). Under semi-intensive pond conditions, modest feed reductions (to 90% or a staged 80%-90%-100% of standard tables) produced similar growth and economic returns to full rations, while slightly decreasing feed cost per kilogram of shrimp, indicating that careful ration control can improve cost efficiency without sacrificing performance.

7.2 Comparison of yield and economic returns

Feeding technologies and strategies that raise growth and yield generally increase gross revenue and shrimp value per hectare. In a 16-week pond trial comparing four feed-management techniques, timer feeders and acoustic demand feeding significantly increased final weights, and the AQ1 acoustic system more than doubled shrimp value to about US\$21,198/ha relative to standard twice-daily protocols (Ullman et al., 2019). A separate study with higher stocking density similarly found that AQ1 demand feeding raised yield to 7430 kg/ha and shrimp value to US\$65,587/ha, clearly outperforming timer and standard feeding while maintaining comparable FCR and survival (Ullman et al., 2018).

Diet formulation, when coupled with appropriate feeding management, can also shift revenues through changes in yield and size distribution. Under commercial conditions, a fishmeal- and fish-oil-free “F3” diet produced higher biomass, better FCR (1.03 vs. 1.15), and larger shrimp, leading to an 11.8% higher sales revenue compared with a commercial reference feed. On-demand feeding with different protein levels showed that although a 40% protein diet was more expensive, it did not improve biomass or economic outcomes relative to 30%-35% protein diets, indicating that overly rich diets may not yield proportional revenue gains when demand feeding is used (Strebel et al., 2023).

7.3 Evaluation of return on investment and economic sustainability

Economic analyses that integrate feed inputs, yields, and market prices show how feeding choices influence return on investment (ROI) and long-term financial viability. In a commercial pond trial comparing conventional and marine-resource-free feeds, the F3 diet yielded higher growth and revenue, resulting in ROI values of 89.8% versus 64.5% for the commercial diet, while all other non-feed costs remained similar between treatments (Tran et al., 2022). Business analyses from Indonesian farms likewise report R/C ratios above 1 and very short payback periods (around 0.5-2.9 years) for intensive *L. vannamei* operations, suggesting that when feed is managed efficiently the sector is highly profitable (Farkan et al., 2024).

Feeding and management strategies also interact with intensification to determine economic sustainability and resource use efficiency. Comparative studies across intensity clusters in India showed that more intensive *L. vannamei* farms achieved higher net returns (about US\$41,641/ha/year) and lower cost per ton, provided feed and other inputs were used efficiently. (Nisar et al., 2021). Multi-country analysis of intensification in Vietnam and Thailand further found that higher-intensity clusters had lower costs per metric ton and greater profitability, reinforcing that feeding strategies which support high yields while controlling feed costs are central to economically sustainable shrimp farming.

8 Case Study: Comparative Evaluation of Different Feeding Strategies in Pacific White Shrimp Farming

8.1 Performance analysis of traditional manual feeding practices

Traditional manual feeding remains a common baseline strategy in pond and tank culture, typically using standard feeding tables and two to four meals per day. Semi-intensive tank and pond trials applying a standard feeding

protocol (SFP) and slight variations ($\pm 10\%$ -20%) showed similar survival, FCR, and economic returns across treatments, indicating that well-calibrated manual tables can support satisfactory growth and profitability without high feed surpluses. At nursery scale in biofloc systems, reducing manual feeding frequency from six to one meal per day did not significantly affect final weight, survival, or FCR, suggesting that in early stages, growth performance can be maintained even with relatively simple manual schedules when water quality is stable (Wasielesky et al., 2020).

Nevertheless, comparative trials consistently show that manual feeding underperforms more intensive or automated strategies in terms of growth and yield. In intensive tanks, a manually fed control group at six meals per day achieved lower final body weight and poorer FCR than groups fed at similar frequencies with automatic feeders, underscoring the limitations of human-timed delivery in matching shrimp appetite patterns (Liang et al., 2025). Large-pond comparisons of manual hand feeding versus automatic timer and acoustic systems also showed the lowest average daily growth, final body weight, and yield under manual regimes, even though survival remained comparable, highlighting that manual feeding is robust but less efficient for maximizing production.

8.2 Production benefits of multiple small-meal feeding regimes

Case studies comparing low versus high feeding frequencies demonstrate clear production gains from multiple small meals. In recirculating systems, automatic feeding 6-12 times per day, with the same total ration as a manual six-meal control, significantly increased final body weight and specific growth rate, while improving FCR; regression analysis indicated an optimal automatic frequency around 7.8 meals per day (Liang et al., 2025). Similarly, post-larval trials showed that feeding six times daily yielded higher final weights than two or four meals, confirming that distributing the ration more finely better matches the shrimp's continuous feeding behavior.

Pond-scale work reinforces these findings by linking increased feeding frequency to higher growth and crop value. In a 16-week pond trial, moving from two daily feedings under an SFP to six feedings via timer feeders raised final individual weights and improved economic returns, even though overall FCR and survival remained similar (Ullman et al., 2019). Subsequent studies in semi-intensive ponds confirmed that higher numbers of meals allow greater total feed inputs and higher yields, with growth responses linked more strongly to the number of meals than to the specific day-night schedule, emphasizing that multiple small meals are a key lever for enhancing production efficiency.

8.3 Economic and environmental assessment of intelligent automatic feeding systems

Intelligent automatic systems—including timer feeders, acoustic demand feeders, and model-based “smart” feeders—offer both economic and environmental advantages over traditional methods. In pond case studies, acoustic demand systems (AQ1) produced the highest final weights, yields, and crop values compared with standard twice-daily SFP and timer-based protocols, while maintaining similar FCR and survival, thereby increasing revenue per hectare without extra feed cost per kilogram of shrimp. Another semi-intensive trial similarly found that on-demand AQ1 feeding yielded larger shrimp and higher production than several fixed over-SFP timer regimes, demonstrating that real-time feedback can outperform pre-set schedules in economic terms (Reis et al., 2020).

Environmental and labor-cost benefits arise from more precise control of ration size and timing. Water-quality monitoring in ponds fed by hand, timers, and AQ1 showed that the acoustic system achieved the greatest yield but also higher late-season ammonia and nitrite, indicating that automated strategies must be matched to system nutrient-processing capacity to avoid water-quality deterioration. In recirculating systems, intelligent feeders using machine-learning biomass prediction can calculate appropriate feed amounts from sensor data in real time, supporting stable water quality while reducing waste and labor, and IoT-linked solar feeders further cut long-term labor and energy costs, achieving large percentage reductions in annual and 10-year operating expenses compared with manual feeding (Boonraksa and Boonraksa, 2025).

9 Conclusions and Future Perspectives

Across culture systems, feeding strategies can be viewed along a spectrum from fixed schedules and ration tables to fully intelligent, sensor-driven control. Fixed-time, fixed-ration approaches remain the backbone of many farms

because they are simple and compatible with standard commercial feeds and protein formulations. They can support good growth and acceptable feed conversion when carefully calibrated, especially when diet quality is high and protein levels match shrimp requirements. At the same time, such strategies are vulnerable to errors in biomass estimation and cannot react to short-term variations in appetite or environmental conditions. More dynamic strategies, including multiple small meals, feed restriction in biofloc or green-water systems, and automated delivery, offer important gains in feed utilization and growth. Studies with reduced feeding rates in biofloc show that moderate restriction can improve both growth and feed efficiency by leveraging natural productivity, while high-protein diets and functional additives further enhance performance. Increasing feeding frequency and using automatic or acoustic demand feeders improves growth and economic returns without compromising survival, indicating that closer matching of feed supply to shrimp demand is a core principle of effective feeding strategies. Intelligent precision approaches based on biomass prediction and IoT platforms are beginning to unify these elements into integrated feeding systems.

Despite substantial progress, existing research on feeding strategies for Pacific white shrimp has several limitations. Many trials are relatively short in duration, focus on a single production phase, or are conducted in experimental tanks and small ponds rather than full commercial farms. This constrains understanding of long-term impacts on pond ecology, sediment dynamics, and multi-cycle sustainability. Moreover, most studies evaluate one dimension at a time—such as protein level, ration size, or feeding frequency—rather than systematically exploring their interactions across different culture intensities and environments. There are also gaps in the evaluation of emerging intelligent and automated technologies. Machine-learning-based biomass prediction and IoT-enabled feeders have demonstrated technical feasibility and good prediction accuracy, but evidence on their robustness across seasons, farm scales, and management styles remains limited. Economic analyses often emphasize feed cost and gross revenue without fully accounting for capital expenditure, maintenance, training, or data-management requirements. In addition, much of the AIoT literature is fish-focused, with relatively fewer shrimp-specific applications, leaving questions about model transferability, behavior-based appetite detection in crustaceans, and integration with health and disease-monitoring systems.

Intelligent precision feeding is poised to become a central pillar of precision aquaculture for Pacific white shrimp. Future systems are likely to couple real-time water-quality sensing, computer vision or acoustic monitoring of feeding activity, and data-driven biomass models to continuously adjust ration size, timing, and spatial distribution. Shrimp-specific machine-learning models that integrate environmental, nutritional, and behavioral data can refine estimates of appetite and growth potential, allowing automatic feeders to minimize overfeeding while sustaining rapid weight gain. As IoT hardware and cloud platforms mature, these tools are becoming more accessible, including for small and medium-scale farms. At a broader scale, intelligent feeding will be increasingly linked to farm-level and even regional management. Integration with AIoT farm-management systems can align feeding decisions with energy use, aeration control, and disease-risk forecasting, improving resilience and lowering environmental footprints. Advances in precision aquaculture point toward multimodal sensor fusion, digital twins, and explainable AI, which could help farmers understand and trust automated recommendations while optimizing FCR, nutrient retention, and economic returns. To realize these prospects, future work must address challenges of cost, interoperability, data quality, and capacity building, ensuring that intelligent precision feeding contributes not only to higher productivity, but also to long-term economic and ecological sustainability of shrimp farming.

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Conflict of Interest Disclosure

The author affirms that this research was conducted without any commercial or financial relationships that could be construed as a potential conflict of interest.

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Feature Review

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Evaluation of Probiotic Applications in Healthy Farming of Grass Carp (*Ctenopharyngodon idella*)

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Abstract Probiotics have emerged as an important strategy for promoting sustainable and healthy aquaculture by improving growth performance, enhancing immunity, and maintaining ecological balance. Grass carp (*Ctenopharyngodon idella*) is one of the most widely cultured freshwater fish species; however, intensive farming practices often lead to microbial imbalance, disease outbreaks, and reduced production efficiency. This review summarizes the application effects of probiotics in grass carp aquaculture, focusing on their regulatory mechanisms and practical benefits. Probiotics can improve feed utilization, stimulate digestive enzyme activities, maintain intestinal microbial homeostasis, and enhance nutrient absorption. Moreover, they contribute to improved antioxidant capacity, immune responses, and resistance against bacterial pathogens. The application of probiotics also plays an important role in regulating water quality by reducing harmful microorganisms and promoting environmentally friendly aquaculture systems. A case study of compound probiotic preparations demonstrates their potential in improving growth performance, intestinal microbiota composition, disease resistance, and economic benefits. Despite these advantages, challenges remain regarding strain selection, functional stability, and precise application strategies. Future research integrating omics technologies and targeted microbial regulation will further promote the development of probiotic-based green aquaculture technologies for grass carp production.

Keywords Probiotics; Grass carp (*Ctenopharyngodon idella*); Intestinal microbiota; Immune regulation; Healthy aquaculture

1 Introduction

Grass carp (*Ctenopharyngodon idella*) is one of the most important freshwater aquaculture species, with very large global production and particular importance in China as an affordable source of aquatic animal protein (Gharti et al., 2023). It is also described as an important economic fish whose germplasm resources are strategically important for the stable supply of high-quality aquatic protein and for the sustainable development of the industry. Projections indicate that grass carp production in China alone may exceed 6.4 million tons by 2030, underscoring the continuing expansion and economic weight of this farming sector. At the same time, aquaculture more broadly remains the fastest-growing animal food production sector and is under increasing pressure to provide food security while improving environmental performance (Fachri et al., 2024). This tension is especially relevant to grass carp culture, because production growth has been accompanied by rising concern over pollution, eutrophication, and resource use, with life-cycle assessment showing that feed processing and water pollution are major contributors to the environmental burden of commercial grass carp production. Farm-level studies also show that culture environment strongly shapes production outcomes: poor pond water quality reduces output, product quality, and profit, whereas improved systems and management can enhance fish quality. Because grass carp is an herbivorous species with distinctive nutritional physiology and high forage intake capacity, healthy farming must integrate suitable feeding, water-quality maintenance, welfare, and disease prevention rather than focus on yield alone (Pedrazzani et al., 2022). This broader healthy-aquaculture perspective is reinforced by welfare-based work showing that nutritional and environmental conditions are directly linked to stress resistance and gut health in cultured grass carp. Even relatively simple production studies in ponds indicate that grass carp can achieve strong growth under different plant-based feeding regimes, but survival, feed conversion, and water-quality stability depend on how culture conditions are managed. Together, these findings show that the

future of the grass carp industry depends not only on maintaining high output, but on shifting from conventional expansion toward healthy aquaculture that balances productivity, fish welfare, environmental control, and product safety.

Despite its scale and value, grass carp farming faces persistent health problems that are intensified by high-density culture and environmental stress. Across aquaculture systems, disease outbreaks remain a major constraint because intensification increases host susceptibility and pathogen transmission. In grass carp specifically, bacterial diseases remain a major threat, and *Aeromonas hydrophila*-associated enteritis alone has been reported to cause substantial economic losses estimated at \$164 million annually. More generally, the rapid development of aquaculture has often been accompanied by environmental degradation, disease emergence, and reduced productivity, creating strong pressure for better health management strategies. Historically, farmers have relied on antibiotics, chemotherapeutics, disinfectants, and other medicinal products to suppress these problems. However, the widespread and sometimes indiscriminate use of these agents has created serious concerns about drug residues, environmental contamination, and selection for antimicrobial resistance in aquaculture settings. Reviews focused on China further show that livestock farming and aquaculture are major areas of antibiotic misuse, with consequences including residue pollution and heightened risks of antibiotic resistance affecting animals and humans. Internationally, antibiotic governance remains uneven: many countries still permit critically important antibiotics in aquaculture, and compliance with international recommendations and certification standards is often incomplete (Luthman et al., 2024). Surveys from freshwater aquaculture likewise indicate that heavy dependence on aquaculture medicinal products can leave gaps in disease management while contributing to public-health and ecosystem risks. At the policy level, current regulatory thinking increasingly emphasizes stricter enforcement, species-appropriate supporting measures, and the development of substitutes for antibiotics rather than continued dependence on them. For grass carp farming, these regulatory and health pressures converge into a practical challenge: producers need disease-control strategies that are effective under pond conditions, compatible with food-safety expectations, and less likely to aggravate antimicrobial resistance or environmental pollution.

Within this context, probiotics have emerged as a promising green technology for healthy aquaculture because they offer a biological route to improve fish performance while reducing reliance on antibiotics and other chemical inputs. Recent reviews consistently describe probiotics as beneficial microorganisms that can enhance growth, feed utilization, immunity, disease resistance, gut microbial balance, and water quality in cultured aquatic animals. Their mechanisms are multifactorial: probiotics can modulate the intestinal microbiota, strengthen innate immune responses, produce antimicrobial substances such as bacteriocins and organic acids, and promote the breakdown of organic matter and toxic metabolites in the rearing environment. These properties make them especially relevant to healthy grass carp culture, where gut health, nutritional efficiency, stress resistance, and pond-water quality are tightly linked. Broad aquaculture syntheses therefore regard probiotics as eco-friendly alternatives to antibiotics that can support disease prevention and environmental sustainability at the same time. Interest has also shifted toward host-associated probiotic strains, because microbes derived from the host or its environment can improve digestion, inhibit pathogen colonization, and stimulate hematological and immune responses more specifically. Among candidate taxa, *Bacillus* spp. have drawn particular attention because they are non-pathogenic, stress tolerant, and associated with improvements in feed utilization, antioxidant defense, immune function, water quality, and disease resistance. Field evidence from freshwater farming also suggests that probiotic and fermented products can reduce disease outbreaks, improve fish growth, lower costs, and decrease dependence on conventional medicinal products. More recent syntheses place probiotics within the wider response to antimicrobial resistance, arguing that they are integral to sustainable aquaculture and to the search for non-antibiotic disease-control strategies. Although practical issues remain, including host specificity, formulation stability, delivery methods, and commercialization, the overall evidence supports probiotics as one of the most promising tools for advancing healthy grass carp farming. Accordingly, evaluating probiotic applications in grass carp is scientifically and practically important for developing culture systems that are more productive, disease-resilient, environmentally responsible, and aligned with the regulatory transition toward greener aquaculture technologies.

2 Types of Probiotics and Their Mechanisms of Action

2.1 Common probiotic species used in aquaculture and their functional characteristics

Probiotics used in aquaculture span several bacterial and yeast groups, including *Lactobacillus*, *Lactococcus*, *Leuconostoc*, *Enterococcus*, *Carnobacterium*, *Shewanella*, *Bacillus*, *Aeromonas*, *Pseudomonas*, and *Saccharomyces*, showing that fish probiotics are taxonomically broad rather than limited to a single lineage. Among these, *Bacillus* spp. are the most consistently emphasized in aquaculture because spore formation improves survival under harsh culture and feed-processing conditions, while their strains are generally described as non-pathogenic and capable of producing antimicrobial compounds (Kuebutornye et al., 2019). *Bacillus* is also valued as both a gut probiotic and a pond bioremediator, since it can degrade organic detritus, reduce nitrogenous waste, and in some species disrupt quorum sensing by degrading AHL signals associated with pathogen virulence (James et al., 2021). Lactic acid bacteria form the second major group, and indigenous finfish LAB such as *Lactobacillus*, *Lactococcus*, *Pediococcus*, *Enterococcus*, *Weissella*, and related genera are regarded as promising because they stimulate digestive function, mucosal tolerance, immune activity, and disease resistance.

Functional selection depends less on genus name alone than on strain-level traits relevant to aquaculture performance. Candidate strains are commonly screened for safety, non-hemolytic behavior, survival under acid and bile exposure, adhesion to mucosal surfaces, extracellular enzyme production, antioxidant capacity, and direct antagonism against pathogens (Coulibaly et al., 2023). In LAB, these traits have been demonstrated in host-associated isolates that survive simulated gastrointestinal conditions, form biofilms, and inhibit multiple pathogens, while also contributing enzymes such as lipases or β -galactosidase that can support digestion. In grass carp and other fish, host-derived strains are increasingly preferred because native probiotics tend to colonize the gut more efficiently and are less likely to disturb microbiota homeostasis than exogenous strains (Chomová et al., 2025). This shift has expanded the range of candidate probiotics beyond classical *Bacillus* and LAB to include autochthonous strains such as *Pseudomonas monteilii* and *Cetobacterium somerae*, both of which have recently shown probiotic potential in grass carp.

2.2 Microbiota regulation

The grass carp intestine contains a complex bacterial community involved in nutrition, host physiology, and immune-related processes, so probiotic action in this species depends first on reshaping an existing microbial ecosystem rather than simply adding one beneficial strain. Dietary probiotics can alter this ecosystem at the community level, and direct feeding trials in grass carp show that oral administration changes bacterial composition at the genus level within weeks. A recurring mechanism is selective enrichment of beneficial taxa: probiotic treatment increased *Cetobacterium* in grass carp, a genus linked to potential immune function, while also favoring other putative beneficial groups such as *Streptococcus* and *Enterococcus* in the intestine (Hao et al., 2017). At the same time, probiotics suppress undesirable members of the microbiota, as shown by reduced intestinal abundance of potential pathogens including *Pseudomonas* and *Flavobacterium* after probiotic feeding.

Microbiota regulation also affects digestive ecology, barrier function, and network stability. In grass carp fed *Bacillus subtilis* Ch9, probiotic supplementation increased total anaerobes as well as *Lactobacillus* and *Bifidobacterium*, supporting the view that *Bacillus* can promote cross-feeding and a more favorable microbial balance instead of acting alone. More recent work with host-derived *Pseudomonas monteilii* JK-1 suggests that probiotic benefits can be mediated through keystone taxa and microbiome network stability, with *Cetobacterium* associated with growth performance and *Akkermansia* associated with immune response (Qi et al., 2024). Probiotics can also support intestinal structure directly: *Cetobacterium somerae* improved digestive and absorptive capacity in juvenile grass carp, reduced intestinal permeability, and preserved tight-junction integrity, indicating that microbiota modulation and epithelial protection are mechanistically linked. This mechanism has limits under environmental stress, however, because nanoplastic exposure in grass carp weakened probiotic protection and altered microbial diversity despite measurable immune activation.

2.3 Immune and disease mechanisms

Probiotics enhance fish disease resistance chiefly through innate immune activation, especially by increasing phagocytic activity, lysozyme production, complement activity, respiratory burst, and cytokine expression. In finfish, lactic acid bacteria often increase neutrophil activity, lysozyme secretion, phagocytosis, and pro-inflammatory cytokines such as IL-1 β , IL-6, IL-8, and TNF- α , although some strains instead preferentially induce IL-10, showing that immune effects are strain and host dependent rather than uniform (Ringø et al., 2018). This host- and strain-specificity is a central feature of probiotic immunobiology in aquaculture, and immune outcomes vary with source, dose, and duration of supplementation. Beyond soluble effectors, probiotics can stimulate gut-associated immunity, including increases in Ig-positive cells and acidophilic granulocytes, thereby strengthening mucosal defense at a major portal of pathogen entry.

Experimental studies show that these mechanisms translate into higher survival after pathogen challenge. In fish fed *Lactococcus lactis*, probiotic supplementation increased growth and survival, upregulated anti-inflammatory cytokines, and moderated excessive pro-inflammatory cytokine responses after *Aeromonas hydrophila* infection. In goldfish, *Exiguobacterium acetylicum* elevated respiratory burst, phagocytosis, antimicrobial enzymes, immunoglobulin levels, and cytokine gene expression, increasing post-challenge survival from 33.2% in controls to 73.2% in the high-dose group. In grass carp specifically, *Pseudomonas monteilii* JK-1 reduced *Aeromonas* load while increasing IL-1 β , IL-10, TNF- α , TGF- β , and antioxidant enzymes in gut and head kidney, linking microbial regulation with coordinated immune and oxidative-stress control. *Bacillus*-based products can extend beyond classical probiotics into adjuvant-like platforms, since recombinant *B. subtilis* spores have enhanced survival and specific IgM and IgZ responses in virus-challenged grass carp, underscoring the broader immunobiological value of *Bacillus* in healthy aquaculture (Soltani et al., 2019). In grass carp, probiotics therefore act through three connected mechanisms: functional taxa selection, intestinal barrier stabilization, and immune priming. These mechanisms make *Bacillus*, LAB, and host-derived strains especially relevant for antibiotic-reduced and health-oriented grass carp farming.

3 Effects of Probiotics on Growth Performance of Grass Carp

3.1 Effects of probiotics on feeding behavior and feed utilization efficiency

Probiotics improve feed utilization in grass carp primarily by strengthening digestive capacity rather than by simply increasing feed intake. In a 6-week trial, a duo-strain preparation of *Bacillus subtilis* and *Lactobacillus plantarum* increased protease, amylase, lipase, and trypsin activities while also lowering feed conversion ratio, indicating more efficient digestion and nutrient use (Luo et al., 2022). A broader review of aquaculture nutrition supports the same mechanism, concluding that probiotics enhance intestinal microbial balance, digestive enzyme activity, food absorption, and ultimately feed efficiency when properly applied.

Evidence from grass-carp-specific trials shows that this nutritional effect can occur with or without major changes in voluntary feed intake. Juvenile fish receiving *Cetobacterium somerae* showed significantly higher feed intake together with improved feed conversion ratio and feed efficiency ratio, suggesting that this host-associated strain promoted both appetite and utilization efficiency (Figure 1) (Chen et al., 2025). By contrast, a multi-strain probiotic improved growth and feed utilization most clearly at 0.34-1.68 g/kg, implying that the quality of nutrient conversion, not maximum consumption alone, explains much of the probiotic growth response.

3.2 Growth parameters and productivity

Across studies, probiotic supplementation consistently improves core growth indicators in grass carp, especially weight gain, specific growth rate, and feed conversion ratio. Dietary supplementation with *Bacillus subtilis* Ch9 for 56 days significantly increased specific growth rate and reduced feed conversion ratio relative to the unsupplemented control. Similar benefits were reported in a 2024 study of host-derived *Pseudomonas monteilii* JK-1, which significantly increased weight gain, specific growth rate, and survival rate while reducing pathogen burden, linking better productivity to better overall health status.

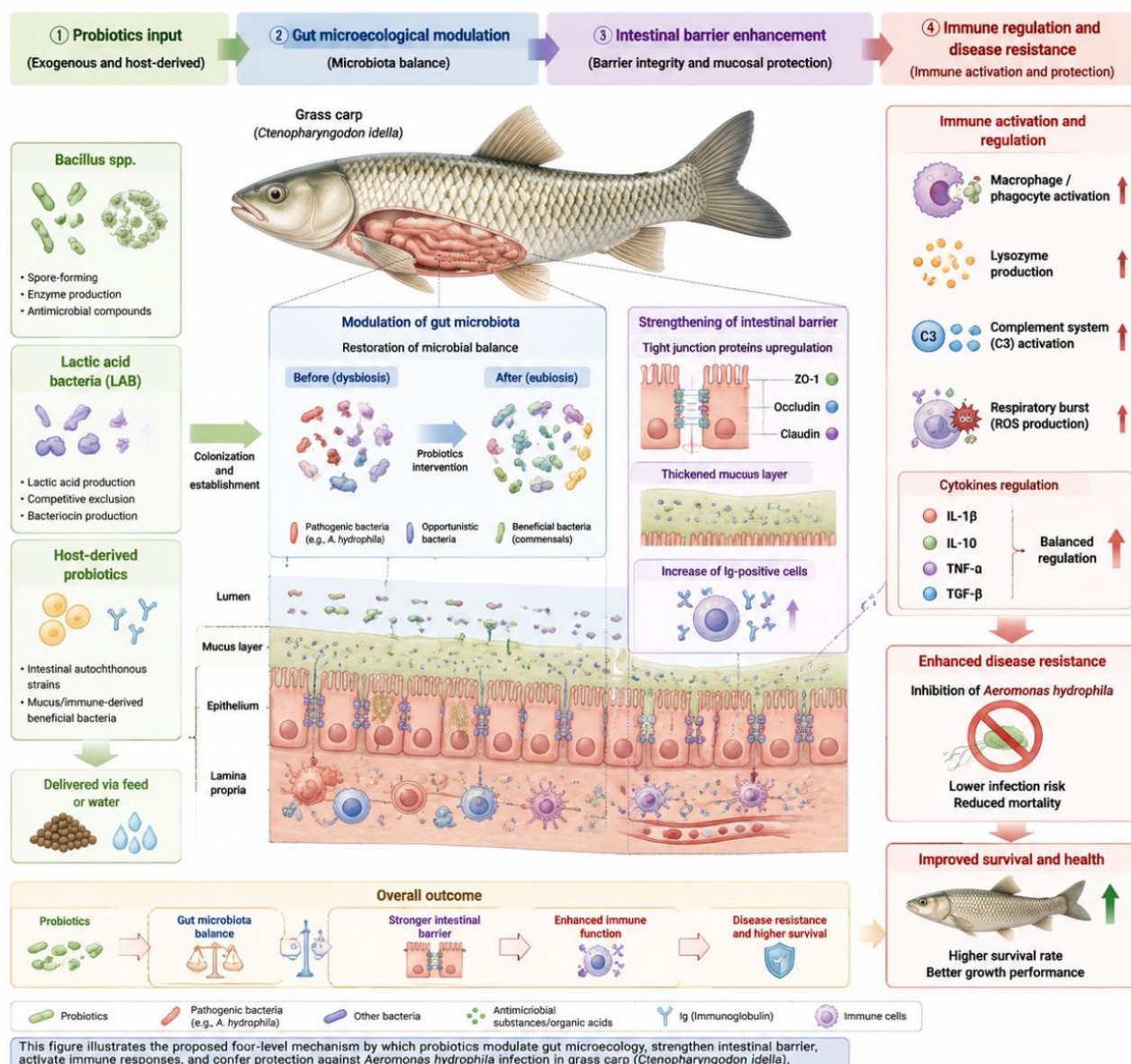


Figure 1 Mechanisms of probiotic-mediated immune enhancement and disease resistance in grass carp (*Ctenopharyngodon idella*)

The productivity benefit is not limited to one probiotic type or one production stage. In fingerling grass carp, diets containing *Bacillus coagulans*, *Rhodopseudomonas palustris*, or *Lactobacillus acidophilus* all increased final weight, daily weight gain, and relative growth rate compared with the control, although differences among the three probiotic treatments were not significant. Likewise, probiotic-fed groups in a comparative feeding study outperformed controls in weight gain and specific growth rate, and the probiotic treatment also improved protein efficiency and food conversion indices, which are directly relevant to aquaculture productivity and cost control (Abdallah et al., 2022).

3.3 Species, dose, and duration

Growth responses depend strongly on probiotic species and dosage, and the best-performing level is often intermediate rather than maximal. With *Bacillus natto*, fish in the Bn3-Bn5 groups showed better growth and lower feed conversion ratio than lower-dose groups and controls, suggesting a threshold concentration is needed before performance gains become clear. However, the response is not indefinitely linear: in grass carp fed host-derived *Bacillus velezensis* LH023, growth improved overall, but after week 5 the 10^8 group grew more slowly than the 10^7 group, indicating that excessive probiotic concentration can reduce the benefit (Liu et al., 2025).

Duration also shapes probiotic outcomes, because physiological gains can appear early and then plateau over longer feeding periods. In the Ch9 trial, digestive enzyme activities rose from days 14 to 56, but the increase was greatest in the shorter term and no longer continued upward by day 56, even though values remained above control fish. A similar pattern of dose optimization was quantified in other studies: broken-line analysis identified about 1.34 g/kg as the optimum level for a multi-strain probiotic, while *C. somerae* produced the best overall growth, intestinal development, and nutrient retention at about $1.27\text{--}1.35 \times 10^9$ cells/kg rather than at the highest inclusion level (Chen et al., 2025). Overall, probiotics improve grass carp growth performance mainly by enhancing digestive efficiency, nutrient retention, and feed conversion, but the magnitude of benefit depends on the probiotic strain, supplementation level, and feeding duration. For grass carp farming, the evidence supports probiotics as effective growth promoters when matched carefully to species-specific and dose-specific conditions.

4 Regulatory Effects of Probiotics on the Digestive System and Nutrient Metabolism of Grass Carp

4.1 Effects of probiotics on intestinal structure integrity and functional improvement

Probiotics improve intestinal structural integrity in grass carp by promoting mucosal development and strengthening epithelial barrier function. In juvenile grass carp, dietary *Cetobacterium somerae* increased intestinal length index, somatic index, and fold height, indicating better intestinal development and a larger absorptive surface. The same study further showed that this probiotic reduced intestinal permeability, preserved tight-junction ultrastructure, and increased tight-junction and adherens-junction biomarkers, supporting a direct role in barrier maintenance rather than only a secondary growth effect (Chen et al., 2025).

Barrier protection is also evident with other host-associated probiotics and under challenge conditions. *Bacillus velezensis* LH023 increased expression of ZO-2, ZO-3, and claudin-12 in the intestine of grass carp, which was interpreted as reduced mucosal permeability and improved protective function (Liu et al., 2025). In infected carp, compound probiotics alleviated villus swelling and prevented the decline of Occludin, Claudin-1, and ZO-1, showing that probiotic barrier support can persist even during pathogen-induced intestinal injury.

4.2 Digestive enzymes and absorption

Probiotics enhance digestive enzyme activity in grass carp across multiple enzyme systems, which helps explain improvements in nutrient digestion and feed use. Feeding *Bacillus subtilis* Ch9 increased protease, amylase, and lipase activities in the intestine and hepatopancreas over 14–56 days, with the best overall response reported at 3×10^9 CFU/kg feed (Wu et al., 2012). Similar species-dependent effects were reported in fingerlings given *Bacillus coagulans*, *Rhodopseudomonas palustris*, or *Lactobacillus acidophilus*, where all probiotics improved growth but *B. coagulans* produced the strongest increase in protease activity.

Improved enzyme activity is closely tied to stronger absorptive function. *C. somerae* enhanced both digestive enzymes and brush-border enzymes in juvenile grass carp, and these changes were accompanied by improved nutrient retention, indicating more effective digestion-to-absorption transfer. This pattern is consistent with broader fish evidence showing that probiotic supplementation improves intestinal microbial balance, digestive enzyme activity, and food absorption, thereby increasing feed efficiency rather than acting only as a passive microbial additive (Assan et al., 2021).

4.3 Metabolism and energy utilization

The metabolic effects of probiotics in grass carp extend beyond digestion to the regulation of lipid deposition, carbohydrate use, and microbial energy metabolism. In fish fed a high-fat diet, *Bacillus subtilis* improved growth and serum biochemical indices while reducing hepatic lipid accumulation, indicating that probiotics can redirect nutrient partitioning away from fatty liver formation (Guo et al., 2022). In parallel, intestinal microbiota studies show that the grass carp gut microbiome itself contributes substantially to nutrition metabolism, with carbohydrate metabolism increasing along the intestine and the hindgut acting as a major site of fiber fermentation that helps the host obtain nutrients and energy from plant material.

Probiotics appear to influence these metabolic processes partly by remodeling microbiota-linked pathways. In grass carp receiving *B. velezensis* LH023, KEGG analysis showed enrichment of pathways related to carbohydrate, amino acid, lipid, cofactor, and vitamin metabolism, suggesting coordinated improvement of nutrient transformation capacity. A complementary signal comes from *C. somerae*, which increased intestinal acetic acid concentration in juvenile grass carp, consistent with enhanced microbial fermentation and better local energy supply for intestinal development and absorption (Chen et al., 2025). Overall, probiotics regulate the grass carp digestive system through barrier reinforcement, enzyme activation, and metabolic reprogramming. These coordinated effects help explain why probiotic supplementation often improves nutrient utilization, intestinal resilience, and growth performance in healthy farming systems.

5 Effects of Probiotics on Immune Function and Disease Resistance of Grass Carp

5.1 Regulatory effects of probiotics on non-specific immune responses

Probiotics enhance the non-specific immune system of grass carp by stimulating humoral and cellular defense indicators that respond rapidly to infection. In a 60-day feeding trial, a multi-strain probiotic increased plasma myeloperoxidase activity and complement C3 content at higher inclusion levels, showing that immune enhancement can be dose dependent rather than identical across all supplementation levels. A separate study using autochthonous intestinal bacteria found that probiotic-fed grass carp had higher respiratory burst, phagocytic activity, and lysozyme activity than controls, together with increased complement C3, total serum protein, albumin, and globulin, indicating broad activation of innate defense pathways.

This immune stimulation is also reflected at the gene-expression level in multiple immune organs. Feeding *Pediococcus pentosaceus* SL001 significantly upregulated IgM and C3 expression in the liver, spleen, and head kidney while downregulating IL-8, suggesting stronger baseline defense with lower inflammatory burden (Gong et al., 2019). Similarly, *Bacillus velezensis* B8 increased serum alkaline phosphatase and SOD activity, and after 3-4 weeks it significantly upregulated IgM and TNF- α in the spleen and kidney, showing that probiotic immunoregulation can intensify over time rather than appear only immediately after feeding begins (Wu et al., 2021).

5.2 Effects of probiotics on antioxidant capacity and stress responses

Probiotics improve antioxidant capacity in grass carp by increasing key enzymatic defenses and reducing oxidative damage. Under *Aeromonas hydrophila* challenge, dietary *Bacillus subtilis* reduced malondialdehyde while increasing total antioxidant capacity, SOD, CAT, GSH, and the expression of antioxidant enzymes including SOD, CAT, and GPx, indicating protection against infection-induced oxidative stress. Comparable effects were observed with duo-strain supplementation of *B. subtilis* and *Lactobacillus plantarum*, which significantly improved SOD and CAT and lowered MDA during a 6-week feeding period, showing that antioxidant benefits are not limited to single-strain preparations (Luo et al., 2022).

These antioxidant effects appear closely linked to stress resilience and intestinal protection. In juvenile grass carp, dietary probiotics including *Bacillus cereus*, *B. subtilis*, *Paracoccus marcusii*, and *Lactobacillus plantarum* elevated serum C3/C4 or AKP, lowered intestinal MDA, and in the *Bacillus* groups activated the Nrf2 pathway while upregulating CAT and SOD-related genes, which supports a mechanistic role for antioxidant signaling (Xue et al., 2020). In the multi-strain trial, probiotic-fed fish also showed lower liver MDA, higher glutathione peroxidase, and a significantly stronger respiratory burst after hypoxia stress, indicating that probiotic-enhanced redox control can translate into better tolerance of environmental stressors.

5.3 Roles of probiotics in enhancing disease resistance and reducing disease incidence

A consistent outcome across studies is that probiotics increase post-challenge survival and reduce disease-related mortality in grass carp. Host-derived *Pseudomonas monteilii* JK-1 significantly increased survival rate and reduced *Aeromonas* pathogen load, while also upregulating IL-1 β , IL-10, TNF- α , and TGF- β in the gut and head kidney, indicating that improved resistance is coupled to coordinated immune activation rather than pathogen suppression alone. Likewise, dietary supplementation with *Lactobacillus buchneri* L3-9 or its extracellular

products significantly reduced mortality after *A. hydrophila* challenge, and the probiotic treatments also decreased Aeromonadaceae and Enterobacteriaceae abundance in the intestine, linking disease control to microbial exclusion of potential pathogens (Gao et al., 2024).

The disease-resistance effect extends across diverse probiotic taxa and delivery strategies. Autochthonous intestinal bacteria reduced cumulative mortality after *A. hydrophila* challenge from 80% in controls to 26.67% in the mixed-strain group, showing that consortia can outperform single strains in protection efficiency. Additional lower-ranked but relevant studies support the same pattern: *Paenibacillus polymyxa* S3 increased survival after *A. hydrophila* infection while upregulating C3, lysozyme, IgM, TLR-4, and MyD88. *Bacillus methylotrophicus* XA-8 also reduced *A. hydrophila* virulence by downregulating aer, act, hylA, lafA, hcp, and luxS, and supplemented fish showed 52.63% infection resistance together with lower intestinal *Aeromonas* abundance (Figure 2) (Khan et al., 2024). Overall, probiotics strengthen grass carp health by improving innate immunity, antioxidant defense, and pathogen resistance. The evidence across many strains supports probiotics as a practical strategy for reducing disease incidence and lowering dependence on antibiotics in healthy grass carp farming.

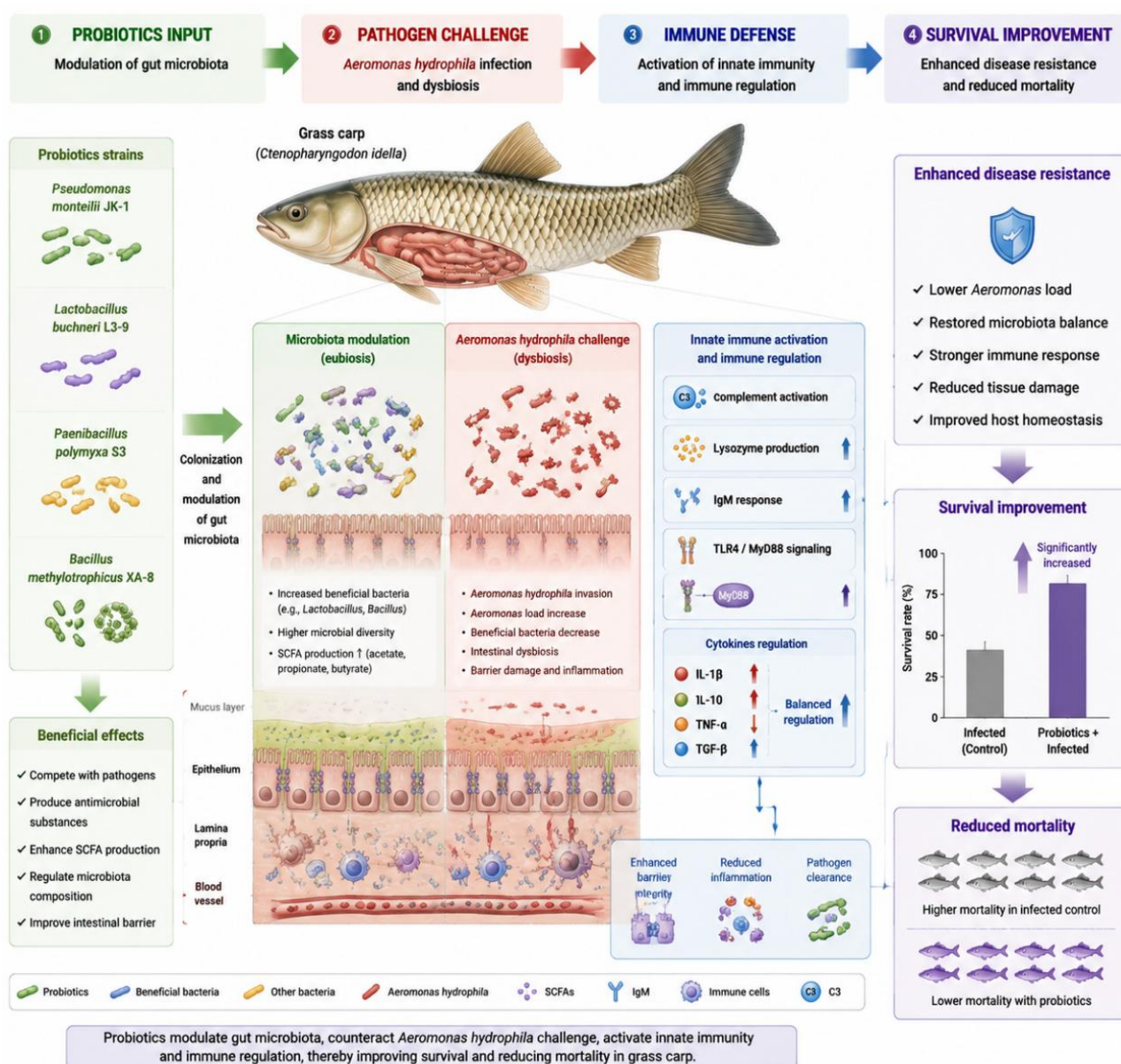


Figure 2 Mechanisms of probiotic-mediated enhancement of disease resistance in grass carp following pathogen challenge

6 Application Effects of Probiotics in Environmental Regulation of Grass Carp Aquaculture

6.1 Effects of probiotics on improving physicochemical properties of aquaculture water

Probiotics can improve the physicochemical properties of grass carp culture water, especially by reducing nitrogenous wastes that drive stress and eutrophication. In grass carp culture, complex probiotics lowered ammonia nitrogen, nitrite nitrogen, and total nitrogen throughout the experimental period, and nitrate nitrogen fell by 54.49% on day 18. A broader freshwater synthesis found that probiotics reduced ammonia by an average of 50.7% across studies, indicating that nitrogen control is one of the most reproducible environmental effects of probiotic application (Nathanailides et al., 2021).

Mechanistically, these effects appear to arise from microbial restructuring and enhanced nitrogen cycling rather than from simple dilution of pollutants. Metagenomic analysis of pond water showed that adding probiotics reduced $\text{NH}_4^+\text{-N}$, $\text{NO}_2^-\text{-N}$, and total nitrogen while increasing nitrification genes such as *amoC_B* and *hao* and denitrification genes such as *nirS* and *nosZ* (Mang et al., 2024). Mixed *Bacillus* systems also improved water quality by reducing $\text{NH}_4^+\text{-N}$, $\text{NO}_2^-\text{-N}$, $\text{NO}_3^-\text{-N}$, and total phosphorus by 46.3%, 76.3%, 35.6%, and 80.3%, respectively, while enriching bacterial groups associated with nitrogen and phosphorus removal.

6.2 pathogen inhibition

Probiotics suppress harmful microorganisms in aquaculture water through several direct and indirect mechanisms, including organic acid production, antimicrobial metabolites, nutrient competition, and exclusion of pathogen colonization. Reviews of disease control in aquaculture show that probiotics can inhibit pathogenic bacteria by lowering pH after organic acid production and by secreting bactericidal compounds such as short-chain fatty acids, peroxide, and bactericidal proteins. Classical probiotic theory in aquaculture also identifies competition for nutrients, energy, and adhesion sites as core mechanisms by which beneficial microbes suppress harmful species in the rearing environment (Verschuere et al., 2000).

In grass carp systems, these antimicrobial effects are supported by strain-specific evidence. *Bacillus methylotrophicus* WM-1, isolated from grass carp culture systems, showed strong antagonism against *Aeromonas hydrophila* and was considered applicable to aquaculture production because it combined pathogen inhibition with environmental safety. More broadly, quorum-quenching probiotics appear especially promising because they reduce bacterial virulence by disrupting quorum sensing rather than by killing pathogens outright, which makes them a plausible non-antibiotic strategy for controlling disease pressure in sustainable aquaculture (Lubis et al., 2024).

6.3 Ecological aquaculture applications

The main value of probiotics in ecological aquaculture is that they can couple production support with environmental remediation. Reviews focused on sustainable aquaculture consistently describe probiotics as feed additives or water supplements that improve water quality, reduce antibiotic dependence, and support environmentally friendly production. In freshwater fish farming, the environmental benefits can outweigh the environmental cost of probiotic production, especially because lower ammonia and improved feed conversion directly reduce the ecological footprint of pond systems (Nathanailides et al., 2021).

Grass-carp-relevant studies also suggest that probiotics fit well within integrated and low-pollution production models, but their use should be embedded in broader management rather than treated as a stand-alone solution. *Bacillus velezensis* LG37 degraded ammonia nitrogen and residual feed protein in grass carp culture wastewater by 55.5% and 73.6% within one week, and it also increased grass carp tolerance to ammonia toxicity. At the same time, recent cyprinid reviews emphasize that probiotic performance depends on environmental factors such as pH, temperature, and dissolved oxygen, and that sustainable aquaculture still requires integrated strategies including water-quality optimization, biosecurity, and preventive health management (Qu et al., 2025). In grass carp aquaculture, probiotics therefore appear most useful as ecological regulators that improve water quality, suppress harmful microbes, and support greener production systems. Their environmental value is strongest when strain selection, application method, and farm management are matched to the specific culture system.

7 Case Study: Evaluation of the Application Effects of Compound Probiotic Preparations in Grass Carp Aquaculture

7.1 Effects of compound probiotic supplementation on growth performance and feed efficiency of grass carp

Compound probiotic supplementation generally improves growth performance and feed utilization in grass carp. In a 6-week feeding trial, a duo-strain preparation of *Bacillus subtilis* and *Lactobacillus plantarum* significantly increased percent weight gain, specific growth rate, and survival rate, while decreasing feed conversion ratio, showing that mixed-strain delivery can enhance both production and feed efficiency. A separate grass carp study using *Lactobacillus buchneri* L3-9 together with its extracellular products also increased weight gain rate and reduced feed conversion ratio within only 21 days, indicating that compound microecological preparations can act rapidly under culture conditions (Gao et al., 2024).

These responses likely reflect complementary functions among strains and bioactive metabolites rather than a simple additive effect. Probiotics are understood to promote growth through improved digestion, enhanced nutrient absorption, and better feed conversion, which is especially relevant in carp farming where feed remains the major production cost. Supporting evidence from other carp models shows that mixed probiotic preparations can reduce feed conversion ratio by 5.04-6.47% and generate measurable feed savings at farm scale, suggesting that the performance gains observed in grass carp are economically meaningful when translated to commercial production (Prazdnova et al., 2025).

7.2 Intestinal microbiota and immune regulation

Compound probiotics regulate the grass carp intestinal ecosystem by enriching beneficial taxa and suppressing potential pathogens. In the duo-strain grass carp study, probiotic feeding increased the relative abundance of Bacteroidetes and Firmicutes while decreasing Proteobacteria and Cyanobacteria, indicating a shift toward a more favorable microbial structure (Luo et al., 2022). Earlier work in grass carp also showed that combined administration of *Shewanella xiamenensis*, *Aeromonas veronii*, and *Bacillus subtilis* increased *Cetobacterium* and reduced potential pathogens such as *Pseudomonas* and *Flavobacterium*, linking microbiota remodeling to lower disease risk.

Immune regulation appears to follow these microbial shifts. Dietary supplementation with *L. buchneri* L3-9 and its extracellular products increased Lactobacillaceae, reduced Aeromonadaceae and Enterobacteriaceae, downregulated the pro-inflammatory gene *TNF- α* , and upregulated anti-inflammatory markers including *TGF- β 1* and *IL-10* (Gao et al., 2024). More broadly in juvenile grass carp, probiotic combinations or multiple candidate strains elevate complement components and antioxidant defenses while improving intestinal barrier-related signaling, suggesting that compound preparations work through coordinated effects on microbiota, mucosal integrity, and innate immunity rather than through one pathway alone.

7.3 Water quality and economic value

The broader value of compound probiotics in grass carp farming lies in coupling host benefits with environmental regulation. Probiotics can improve freshwater pond conditions by lowering ammonia, nitrite, and organic loading, and average effects across freshwater fish studies include a 50.7% reduction in ammonia and a 10.7% decrease in feed conversion ratio, both of which directly support more sustainable production. Mechanistically, water-applied probiotics can promote nitrification and denitrification by increasing functional genes such as *amoC_B*, *hao*, *nirS*, and *nosZ*, which explains why improvements in water quality often persist beyond the immediate feeding response (Mang et al., 2024).

Although direct pond-scale case studies in grass carp remain fewer than feed-based trials, related high-density carp systems show the same integrated pattern of benefit. In crucian carp, long-term use of compound probiotics under micro-water-exchange conditions kept total ammonia nitrogen and nitrite in dynamic equilibrium, improved body weight and length, and lowered mortality after bacterial challenge. Likewise, probiotic use in biofloc-based carp culture reduced $\text{NH}_3\text{-N}$ and NO_2^- , improved growth and welfare, and supports the conclusion that compound

probiotics can contribute to ecological aquaculture by reducing waste output, stabilizing culture water, and improving the economic efficiency of feed use (Ajamhasani et al., 2023). In this case-study perspective, compound probiotic preparations show clear potential to improve growth, gut health, and system sustainability in grass carp aquaculture. Their most practical value appears when feed efficiency, immune stability, and water-quality management are evaluated together rather than as isolated outcomes (Figure 3).

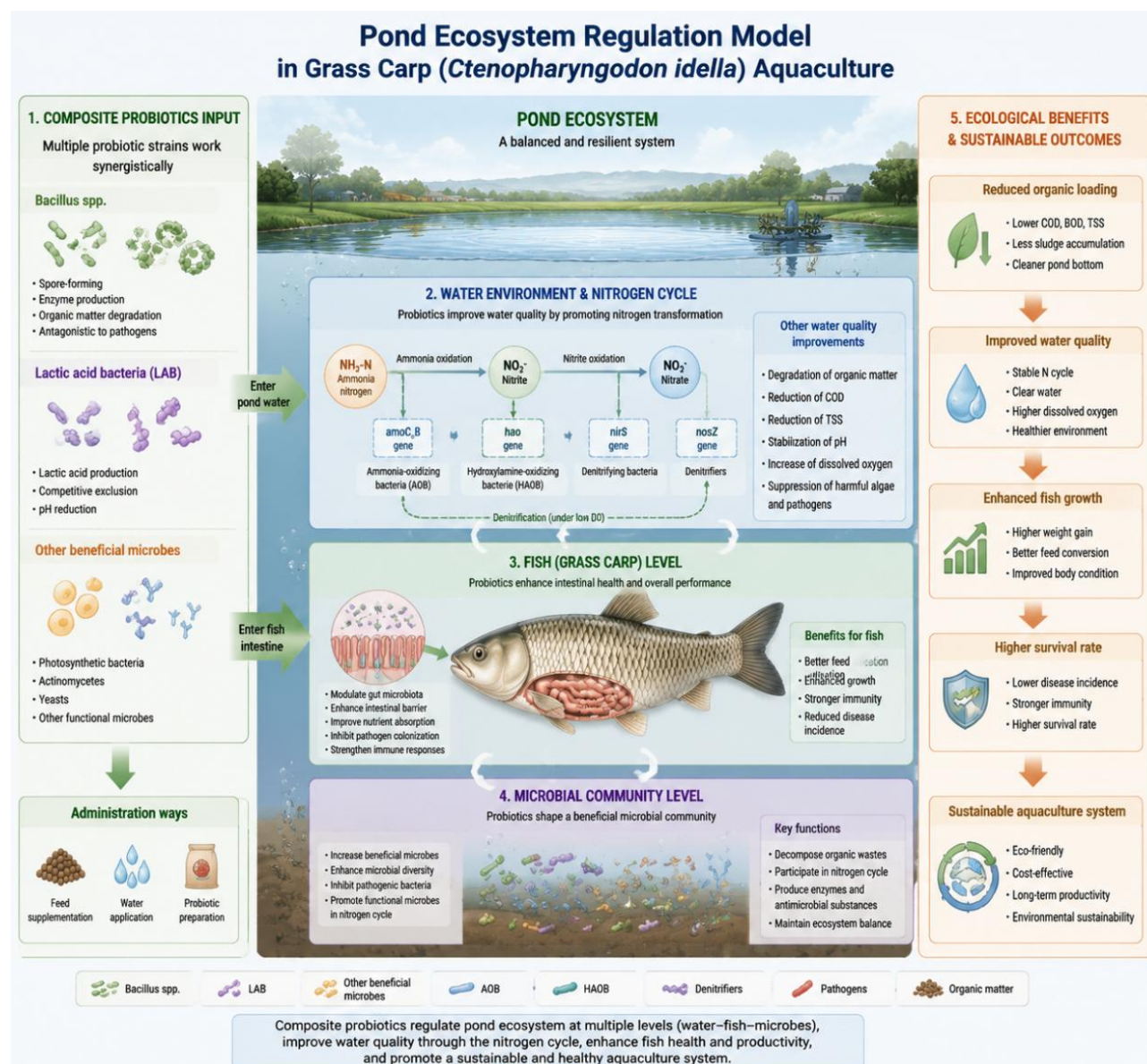


Figure 3 Ecological regulation mechanisms of compound probiotics in grass carp aquaculture system

8 Key Issues and Future Perspectives of Probiotic Applications

8.1 Probiotic strain selection, functional evaluation, and optimization of stability

A core issue in future grass carp probiotic development is that strain efficacy is species- and environment-dependent, so candidate strains cannot be selected only by taxonomic identity. Reviews of aquaculture probiotics emphasize that a strain beneficial in one host may not provide the same benefit in another, and may even become unsuitable under different rearing conditions, which makes extensive host-oriented testing essential before field use. This concern is consistent with newer overviews stressing that strain selection for aquaculture must account for safety, functional performance, and species-specific dosing, because predictable large-scale application remains a major bottleneck (Elsegeny et al., 2025).

Future screening should therefore combine biosafety evaluation with functional trait testing and formulation-oriented stability assessment. Candidate strains are now expected to show tolerance to low pH, bile or salinity stress, antagonism toward pathogens, non-hemolytic behavior, and preferably traits such as adhesion or sporulation that support colonization and storage stability. Recent work on indigenous aquaculture isolates also shows that pH tolerance, salinity resilience, gut colonization potential, and spore formation can be integrated into trait-based ranking systems, with sporulation being especially useful for feed formulation, storage, and administration stability (Rwezawula et al., 2025).

8.2 Synergistic applications with feed, water, and culture systems

The next stage of application in grass carp farming is likely to depend less on single additives and more on synergistic integration with feeds, water management, and farming systems. Recent reviews indicate that multi-strain probiotics and synbiotics often outperform single strains, and broader evidence across aquaculture shows superior efficacy of multi-strain or synbiotic strategies in 68% of trials for growth and disease resistance (Wen et al., 2026). This matters for grass carp because practical farming systems must improve several outcomes at once, including feed utilization, intestinal health, pathogen control, and water quality.

Evidence from carp and pond-system studies suggests that probiotics work best when they are matched with the production environment rather than added in isolation. In biofloc culture, combining probiotics with complex carbon sources improved ammonia, nitrite, growth, and welfare indices, showing that probiotic function can be amplified by system design and substrate availability (Ajamhasani et al., 2023). Field-oriented reviews focused on grass carp also report that water-applied probiotics such as *Pseudomonas stutzeri* and *Bacillus* strains reduced ammonia, nitrite, and total nitrogen while reshaping ambient microbial communities, supporting integration of probiotics into ecological water regulation strategies.

8.3 Precision regulation through omics

A major future direction is to move from outcome-based evaluation to mechanism-based precision regulation using genomics, metagenomics, transcriptomics, and metabolomics. Probiogenomics has been proposed as a framework for characterizing probiotic candidates through whole-genome sequencing, which can identify metabolic capacity, stress-resistance traits, and genes linked to adhesion, bacteriocin production, and immunomodulation (Fachri et al., 2024). More broadly, multi-omics integration is increasingly favored because single-omics approaches can miss regulatory links across microbial composition, host responses, and metabolite production.

For grass carp specifically, omics tools are especially promising because the intestinal microbiome already has identifiable functional structure that could guide probiotic targeting. Multi-omics work in grass carp showed that Proteobacteria and Fusobacteria/Firmicutes/Bacteroidetes form two ecological and functional groups with different capacities for carbohydrate utilization, virulence, and antibiotic resistance, and the proposed Functional Group 2/Functional Group 1 ratio may serve as a biomarker for microbiota status (Li et al., 2023). Parallel fish studies further show that combined metagenomics, metabolomics, and transcriptomics can link probiotic-induced microbial shifts to specific metabolic pathways and host phenotypes, providing a model for precision probiotic design in grass carp. Overall, the future of probiotics in healthy grass carp farming lies in selecting host-adapted stable strains, embedding them into integrated feed-water-system management, and using omics tools to predict and monitor function. These advances should make probiotic application more standardized, more mechanistically transparent, and more reliable at commercial scale.

9 Conclusions and Future Perspectives

Probiotics have emerged as one of the most promising biological tools for improving the health and production performance of grass carp aquaculture. Across existing studies, their major functions can be summarized as promoting growth, improving feed utilization, enhancing digestive enzyme activity, maintaining intestinal epithelial integrity, regulating gut microbial balance, and strengthening non-specific immune responses. These effects are closely interconnected. Improved intestinal structure and digestive function increase nutrient

assimilation, while a more stable intestinal microbiota helps suppress opportunistic pathogens and supports mucosal homeostasis. At the same time, probiotics stimulate antioxidant defenses and innate immune factors, thereby increasing the resilience of grass carp under intensive farming conditions. Beyond their direct effects on the host, probiotics also play an important regulatory role at the culture-system level. By reducing ammonia, nitrite, and other harmful metabolites, and by reshaping microbial communities in water, probiotics contribute to a healthier aquaculture environment that lowers physiological stress and disease pressure. This dual action on both fish and water makes probiotics especially valuable in healthy grass carp farming, where sustainable productivity depends not only on rapid growth but also on ecological stability, reduced antibiotic reliance, and improved survival. Therefore, probiotics should be regarded not merely as feed additives, but as multifunctional biological regulators that connect nutrition, immunity, environmental management, and green production.

Despite the encouraging progress, current research on probiotic application in grass carp still has several important limitations. First, many studies remain focused on short-term feeding trials and phenotypic observations, while the long-term effects on host health, ecological safety, and farming-system stability remain insufficiently clarified. Second, the responses of grass carp to probiotics are strongly influenced by strain specificity, dosage, developmental stage, feed composition, and environmental factors such as temperature, dissolved oxygen, and water quality. As a result, probiotic effects observed under laboratory or small-scale conditions are not always fully reproducible in commercial aquaculture settings. In addition, many candidate probiotics currently used in aquaculture are not host-associated strains, which may limit their colonization ability, stability, and functional consistency in the grass carp intestinal tract. Technological and industrial constraints also restrict broader application. The screening and functional verification of superior strains remain difficult, especially when safety, antagonistic activity, digestive contribution, immune regulation, and environmental adaptability must all be evaluated together. Standardized protocols for strain selection, product formulation, dosage control, storage stability, and delivery methods are still lacking. At the same time, large-scale production of highly active and stable probiotic products remains a challenge, particularly for formulations intended for diverse aquaculture environments. Regulatory uncertainty, biosafety assessment, and the need to prevent unintended ecological impacts further complicate practical deployment. These limitations indicate that the transition from experimental success to standardized and reliable field application is still incomplete.

Future development of probiotic-based green aquaculture technologies for grass carp will likely move toward greater precision, integration, and ecological orientation. One major trend is the selection of host-adapted and functionally targeted strains, especially those derived from the grass carp intestine or culture environment, because such strains are more likely to colonize effectively and perform consistently. At the same time, probiotic development will increasingly emphasize multi-strain formulations, synbiotic combinations, and coordinated use with feed management, water regulation, and ecological farming systems such as biofloc or low-exchange aquaculture. This systems-based approach is expected to improve not only fish growth and disease resistance but also nutrient recycling, microbial stability, and overall environmental performance of production systems. Another important trend is the use of omics-based technologies to uncover the precision regulation mechanisms of probiotics. Genomics, metagenomics, transcriptomics, and metabolomics can help identify functional strains, predict biosafety, reveal host-microbe interactions, and clarify how probiotics influence immunity, metabolism, and microbial network assembly in grass carp. These tools will support the development of next-generation probiotics, paraprobiotics, postbiotics, and even engineered microbial platforms with improved stability and targeted function. In the future, probiotic technology in grass carp aquaculture is likely to evolve from empirical supplementation toward data-guided microbial management. Such a transition will provide stronger support for antibiotic-free farming, environmentally friendly production, and the construction of resilient green aquaculture systems. In conclusion, probiotics have become an important foundation for promoting healthy, efficient, and sustainable grass carp aquaculture. Their future value will depend on whether research can move beyond broad efficacy claims toward standardized, mechanism-based, and field-validated application systems.

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Conflict of Interest Disclosure

The author affirms that this research was conducted without any commercial or financial relationships that could be construed as a potential conflict of interest.

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Research Insight

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Health Management Strategies for Large Yellow Croaker During High-Temperature Seasons

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Abstract High-temperature stress has become one of the most critical environmental constraints affecting marine aquaculture under ongoing climate warming, particularly for economically important species such as large yellow croaker (*Larimichthys crocea*). This review synthesizes current knowledge on the impacts of elevated temperature on physiological functions, disease susceptibility, and overall health performance of large yellow croaker, and evaluates integrated management strategies for mitigating thermal stress in aquaculture systems. High temperatures disrupt metabolic homeostasis, leading to increased energy expenditure, impaired respiratory and osmoregulatory functions, and reduced growth efficiency and feed utilization. At the immune level, thermal stress weakens host defense mechanisms, alters inflammatory responses, and promotes gut microbiota dysbiosis, thereby increasing the risk of bacterial and viral disease outbreaks. In response, environmental regulation strategies such as water temperature control, dissolved oxygen optimization, and water quality management are essential for maintaining system stability. Nutritional interventions, including optimized protein-energy balance and functional feed additives such as probiotics and immunostimulants, further enhance stress resilience. In addition, advances in health monitoring and early warning technologies, including physiological indicators and molecular diagnostics, provide new opportunities for precision aquaculture management. This review highlights the importance of integrated “environment-nutrition-management” frameworks and proposes future directions for intelligent and climate-resilient aquaculture systems for large yellow croaker.

Keywords High-temperature stress; Large yellow croaker; Marine aquaculture; Health management; Climate change

1 Introduction

Large yellow croaker (*Larimichthys crocea*) is one of China's most important marine aquaculture species, highly valued for its taste, nutritional quality, and strong market demand, and its cage-culture production has led the national marine fish sector for many years. However, rapid expansion of its farming has been accompanied by germplasm degradation, reduced disease resistance, and inconsistent product quality, threatening sustainable development of the industry (Han et al., 2025). As a warm-water coastal species with an optimal temperature of about 18 °C-25 °C and relatively high water-quality requirements, large yellow croaker is particularly sensitive to environmental fluctuations common in intensive mariculture. At the same time, intensive stocking and environmental change have driven frequent outbreaks of parasitic and bacterial diseases, making health constraints a central bottleneck for this species (Yao et al., 2024).

Rising water temperature linked to climate variability adds a further layer of risk to marine aquaculture systems. Comprehensive thermal biology assessment of cultured large yellow croaker shows that, although this species has relatively wide thermal limits and apparent plasticity, long-term exposure to 30 °C triggers energy redistribution, oxidative stress responses, and significant reductions in body weight, indicating trade-offs between growth, health, and heat tolerance under chronic heat stress (Wu et al., 2022). In floating sea-cage systems, shallow culture depth, high densities and limited space constrain behavioral thermoregulation and increase risks of hypoxia and disease infection during warm periods, leaving farms in main producing areas already at risk from summer heatwaves with in situ sea surface temperatures surpassing 30 °C. Case studies from other marine fish demonstrate that prolonged high temperatures (e.g., 35 °C in spotted seabass or extreme summer conditions in carp) precipitate oxidative damage, inflammation, and elevated mortality, highlighting generic mechanisms by which heat stress undermines

fish health (Yang et al., 2024). For large yellow croaker, farm-level comparisons indicate that cage-reared fish can experience prolonged summer temperatures above the optimal range, accompanied by lower dissolved oxygen, higher mortality and poorer growth than fish maintained in mobile offshore ship systems that can track more favorable environmental conditions. International experience further shows that marine heatwaves and elevated temperatures can intensify harmful algal blooms and secondary infections, leading to geographically extensive fish kills and revealing the vulnerability of shallow, warm-water ecosystems where cultured fish often live near their upper thermal limits.

Within this climatic and environmental context, infectious diseases have become a major limiting factor for large yellow croaker aquaculture. Ciliate parasites such as *Cryptocaryon irritans* and scuticociliates are capable of causing rapid outbreaks, abnormal behavior, severe tissue damage and high cumulative mortalities in farmed stocks, with infection dynamics strongly influenced by stocking density and mariculture conditions. Recent investigations in large yellow croaker have documented mass-mortality events linked to scuticociliate infection, with experimental challenges producing over 70% cumulative mortality within one week, and transcriptomic analyses revealing extensive immune and metabolic disruption at the peak of mortality. Coinfections with blood-borne and myxosporean parasites have also been associated with mass mortalities in offshore net-cage systems, with year-round feeding and seasonal fish movements likely facilitating parasite circulation and transmission (Zhang et al., 2025). At the same time, bacterial pathogens such as *Vibrio* spp. and *Pseudomonas plecoglossicida* remain economically important, with outbreaks occurring across temperature ranges and sometimes outside previously recognized seasonal windows, underscoring the dynamic interaction between pathogens, host susceptibility, and changing environmental conditions. More broadly, infectious disease is recognized as a leading global constraint in aquaculture, causing multibillion-dollar losses annually, with disease emergence and antimicrobial resistance making traditional, treatment-focused approaches increasingly unsustainable (Wright et al., 2023).

These converging pressures make health management during high-temperature seasons a strategic priority for the large yellow croaker industry. General aquaculture experience emphasizes that the most predictable consequence of stress is immune suppression, leading to increased disease susceptibility and mortality, and therefore highlights the importance of controlling environmental stressors such as temperature, dissolved oxygen and stocking density through good husbandry and biosecurity practices rather than relying solely on therapeutic interventions. Preventive health strategies—combining optimized culture systems that avoid peak thermal stress, farm-level biosecurity, vaccination where available, functional feeds and probiotics, and microbiome-informed early-warning tools—are increasingly viewed as essential components of sustainable disease control frameworks that align with One Health principles. For large yellow croaker specifically, research on probiotics capable of inhibiting key bacterial pathogens, breeding for enhanced stress and temperature tolerance, and alternative farming systems that maintain fish within optimal thermal and oxygen ranges illustrate emerging pathways to strengthen resilience under warming scenarios. Systematically synthesizing these strands into health management strategies tailored to high-temperature seasons is therefore of great significance for safeguarding fish welfare, stabilizing production, and securing the long-term sustainability of large yellow croaker aquaculture.

2 Research Background and Mechanisms of High-Temperature Stress

2.1 Climate warming and marine heatwave ecological context

In recent decades, global ocean warming has driven a marked rise in the frequency, duration and intensity of marine heatwaves (MHWs), with the number of MHW days roughly doubling between 1982 and 2016. These extreme warm events are projected to intensify strongly under continued warming, greatly increasing the probability that coastal farming areas experience prolonged high-temperature anomalies. MHWs already cause broad ecological impacts, restructuring marine ecosystems and threatening biodiversity and ecosystem services that support fisheries. For exploited fish and invertebrates, annual high temperature extremes typically reduce biomass for most stocks and lower maximum catch potential, adding to long-term climate impacts (Cheung et al., 2021).

MHW impacts in productive boundary regions, such as the northeast Pacific, illustrate how biomass declines and rapid range shifts during heatwaves can be several times larger and faster than those driven by gradual warming alone. Such events impose “double strains” on fisheries management by overlaying acute shocks on chronic warming trends (Cheung and Frölicher, 2020). For aquaculture species, including large yellow croaker, extreme temperature episodes are becoming more frequent and intense, and temperature acts as the master abiotic factor controlling development and physiology across all life stages. Climate change-induced extremes drive changes in growth, metabolism, hemato-physiology and immune function, with impacts varying among species and depending on stress magnitude. Large yellow croaker farms in China’s main production areas are already close to or within risky temperature regimes during summer. Field data show maximum sea surface temperatures around 30.1 °C and rapid warming rates in summer, exposing cage-reared croaker to summer heatwaves (Wu et al., 2022). Although thermal safety margins relative to lethal limits appear currently positive, prolonged exposure to 30 °C induces energy redistribution, oxidative stress, and reduced body weight, indicating sublethal performance costs under chronic heat.

2.2 Physiological and cellular mechanisms of thermal stress

At the organismal level, temperature increases act as potent acute and chronic stressors for fish. Rapid warming elicits typical primary and secondary stress responses, including catecholamine and cortisol release, followed by rises in blood glucose and lactate, and changes in osmolality and hematological variables. These reactions are superimposed on elevated metabolic rate under chronic warming, potentially compromising the capacity to cope with additional stressors and leading to long-term impacts on fitness. Acute upper thermal limits are governed by direct thermal effects on reaction rates, protein structures and membrane fluidity, which then propagate through cellular and organ-level pathways. In fish, these mechanisms include mitochondrial dysfunction, oxygen limitation in some species, and impaired excitability of neural and muscular cells, leading to loss of equilibrium, failed homeostasis and ultimately heat death (Ern et al., 2023).

The limiting pathways vary among species, life stages and thermal histories, implying that a single universal failure mechanism is unlikely. At the cellular level, high temperature commonly induces oxidative stress, inflammation and apoptosis. In rohu carp, partial-lethal thermal exposure elevates antioxidant defenses (e.g. reduced glutathione, catalase, superoxide dismutase expression) and heat shock responses (hepatic hsp70), yet these responses are insufficient to prevent lipid peroxidation, DNA fragmentation, and pro-inflammatory activation, leading to hepatotoxicity and partial mortality. Similarly, in pufferfish, high temperature elevates serum enzymes, triggers oxidative damage, and upregulates pro-apoptotic genes (p53, caspase-9, caspase-3), indicating caspase-dependent and p53-mediated apoptosis under thermal stress. For large yellow croaker, prolonged exposure to upper-range temperatures (e.g. 30 °C) results in energy reallocation and oxidative adjustments. Experimental work shows that long-term high temperature reduces body weight and increases superoxide dismutase activity in gills, reflecting a trade-off between maintaining performance and mitigating oxidative stress (Wu et al., 2022). At the proteomic level, high-temperature stress in croaker liver alters thousands of proteins, with 442 differentially expressed proteins enriched in pathways related to translation, oxidative phosphorylation, ribosomes and lipid metabolism, indicating broad reprogramming of protein synthesis and energy use (Figure 1).

2.3 Overview of thermal stress response pathways in aquatic animals

Aquatic animals mount a conserved cellular stress response to temperature extremes that is centered on heat shock proteins (HSPs). In fish and shellfish, HSP families such as HSP70 and HSP90 act as molecular chaperones for protein folding, assembly, and protection against misfolding, and are upregulated not only by heat but also by hypoxia, toxins and infection. The HSP response contributes to thermotolerance and also modulates apoptosis, inflammation and immune function, linking environmental stress to disease resistance in finfish and shrimp (Jeyachandran et al., 2023). In teleost fish generally, HSP expression is induced in numerous tissues and cell types by both biotic (pathogens) and abiotic (heat, cold, contaminants) stressors, and is now recognized as a central component of the generalized stress response. In aquaculture, non-traumatic induction of HSPs (e.g. by mild heat or stimulants) is being explored as a strategy to enhance resilience, reduce handling trauma, and support vaccination and transport. For large yellow croaker specifically, multiple thermal stress pathways have been characterized.

Genome-wide analyses have identified 17 hsp70 genes organized into distinct evolutionary groups, with several showing significant upregulation under heat stress, indicating diversified but coordinated HSP-mediated defenses against temperature challenges. Liver transcriptome studies under heat and cold stress further reveal thousands of differentially expressed genes, with strong enrichment of energy metabolism and related pathways, confirming that temperature stress reshapes metabolic and stress-response networks at the transcriptional level. Signal-transduction cascades such as p38 MAPK also participate in croaker thermal responses.

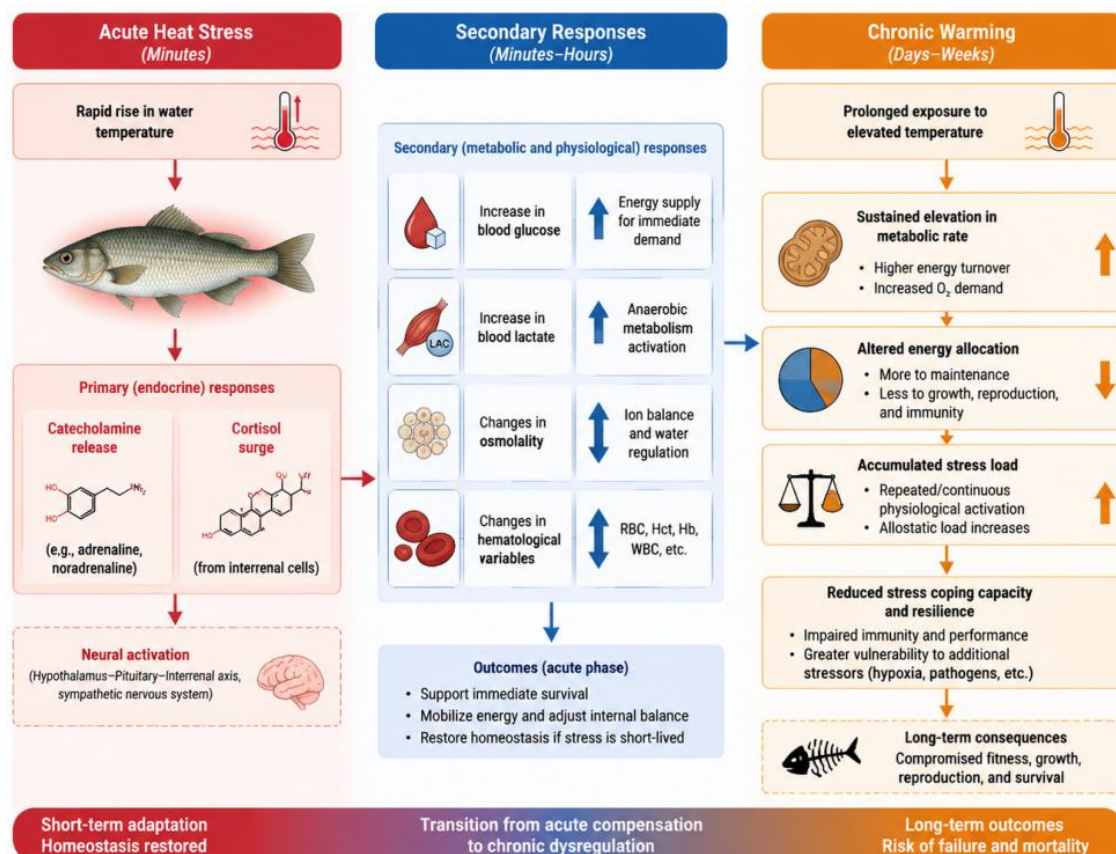


Figure 1 Organismal stress response pathways in fish under acute and chronic thermal stress

Note: Acute warming triggers endocrine activation (catecholamines and cortisol), followed by secondary metabolic responses, while chronic exposure leads to sustained metabolic elevation and reduced stress coping capacity

In a croaker kidney cell line, both cold (10 °C) and heat (35 °C) significantly upregulate p38 MAPK transcripts, and thermal exposure increases p38 phosphorylation together with transcription of HSP27 and caspase-3. Pharmacological inhibition of p38 MAPK suppresses HSP27 and caspase-3 induction, indicating that p38 mediates key branches of the heat shock and apoptotic response in this species. Genetic studies also show that acute heat tolerance (AHT) in large yellow croaker is polygenic, with genome-wide association identifying several significant SNPs and ~30 candidate genes, including heat shock factor 1, DnaJ homologs, Hikeshi and protein disulfide-isomerase A3 (Wu et al., 2021). Comparative analyses highlight the roles of blood-vessel regulation, heat shock response and endoplasmic reticulum stress response in inter-individual variation in AHT, providing a mechanistic basis for breeding heat-tolerant strains.

High-temperature seasons now unfold against a background of intensified marine heatwaves and chronic warming, exposing large yellow croaker to more frequent and severe thermal stress. At the organismal, cellular and molecular levels, heat challenges induce complex stress, oxidative, apoptotic and heat shock pathways that reshape metabolism and compromise growth and health. In large yellow croaker, detailed characterization of thermal limits, transcriptomes, proteomes, signaling cascades and genetic determinants of heat tolerance provides a solid mechanistic foundation for targeted health-management and selective-breeding strategies under a warming ocean.

3 Effects of High Temperature on Physiological Functions of Large Yellow Croaker

3.1 Changes in metabolic rate and energy allocation

High temperature reshapes liver metabolism of large yellow croaker, shifting how energy is produced and allocated. Proteomic analysis under high-temperature stress shows reduced protein synthesis and a transition from oxidative phosphorylation to glycolysis, alongside increased fatty acid biosynthesis and reduced fatty acid catabolism in the liver of thermally stressed fish (Zhang et al., 2023). Transcriptomic work further confirms that temperature stress in large yellow croaker broadly alters energy-metabolism pathways, with genes encoding key metabolic enzymes markedly up- or down-regulated in the liver.

Long-term exposure to high rearing temperatures redistributes energy away from somatic growth toward defense and maintenance. In large yellow croaker acclimated to 30 °C, body weight declines while oxidative stress markers such as gill superoxide dismutase activity increase, indicating a trade-off between growth and heat tolerance. Multi-omics analysis under summer heat shows that dietary inulin can partially rebalance this allocation by upregulating hepatic glycolysis and fatty-acid biosynthesis and enriching beneficial gut bacteria, thereby supporting energy production and growth under chronic thermal stress (Yin et al., 2026).

3.2 Disruption of respiration and osmoregulatory functions

High water temperature challenges gill function in teleosts, combining respiratory strain with osmoregulatory disturbance. In Atlantic salmon smolts, rapid warming to 24 °C in seawater causes complete mortality and severe ion-regulatory failure, with poor plasma ion control and depressed gill Na^+/K^+ -ATPase activity, highlighting a temperature threshold beyond which osmoregulation collapses. Similar enzyme suppression occurs in juvenile goldfish, where elevated temperatures reduce gill Na^+/K^+ -ATPase expression while inducing structural lesions such as lamellar fusion and epithelial detachment, implying impaired gas exchange and ionic balance under heat stress (Ngozichukwu and Rahman, 2025).

Transcriptomic analysis in Siberian sturgeon gills illustrates the mechanistic basis of these osmoregulatory disturbances. Heat stress elevates reactive oxygen species and tissue damage, while downregulating Na^+/K^+ -ATPase α and upregulating multiple ion-transport genes involved in active ion absorption and passive efflux, indicating increased gill permeability and compensatory ion-transport adjustments (Yang et al., 2023). In other species, high-temperature exposure elevates antioxidant enzymes and heat-shock proteins in gills, yet oxidative and nitrative damage still develops, underscoring that respiratory and osmotic homeostasis remain vulnerable when temperatures exceed adaptive limits (Schleger et al., 2024).

3.3 Decline in growth performance and feed utilization efficiency

Long-term high temperatures generally depress growth performance once the thermal optimum is exceeded. In hybrid catfish, growth and feed utilization follow a quadratic response to temperature: performance peaks around 32 °C but falls sharply at 37 °C, where growth, feed efficiency, and tissue condition all deteriorate (Khieokhajokhet et al., 2022). Studies on cherry salmon show a similar pattern: body weight, growth rate, feed intake, and feed efficiency are significantly higher at cooler 10 °C-14 °C than at 18 °C-22 °C, with 22 °C associated with poor feeding and impaired growth and health (Lee and Balasubramanian, 2023). These performance declines are tightly linked to metabolic costs and feed conversion. In cherry salmon, reduced feed efficiency at elevated temperatures is attributed to increased standard metabolic rate, which leaves less dietary energy available for growth under fixed ration sizes. Across other cultured species, higher rearing temperatures can require more feed per unit biomass gain and worsen nutrient deposition, as seen in growth-hormone transgenic Atlantic salmon reared at 16.5 °C, which show poorer feed conversion and less efficient omega-3 deposition than fish at cooler temperatures.

High temperatures in large yellow croaker culture shift liver metabolism toward glycolysis and altered lipid use, while long-term warming forces an energy trade-off away from growth and toward stress defense. Gill respiration and osmoregulation become fragile under heat, with Na^+/K^+ -ATPase suppression, structural damage, and oxidative stress compromising gas exchange and ion balance. Across species, exceeding optimal temperatures consistently reduces growth performance and feed efficiency by raising metabolic costs and impairing nutrient utilization, highlighting the need to manage summer temperatures carefully in large yellow croaker aquaculture.

4 Disease Occurrence and Immune Alterations under High Temperature

4.1 Characteristics of bacterial and viral disease outbreaks

In large yellow croaker cage culture, bacterial diseases show clear seasonality, with vibriosis occurring mainly from June to October and peaking in July-August when water temperature is high; mortality can reach 30%-40%, and even 80% in severe cases. Under these warm, crowded conditions, *Vibrio alginolyticus* and *V. harveyi* proliferate, and high stocking density, environmental deterioration, and skin damage at high temperature are identified as major drivers of outbreaks.

Other pathogens show temperature-linked patterns that are crucial for health management. Visceral white nodule disease (VWND) caused by *Pseudomonas plecoglossicida* usually occurs at 16 °C-19 °C, but a virulent strain was shown to trigger outbreaks even at 12 °C, expanding the known risk window (Li et al., 2020). Temperature-dependent parasitic diseases have also been documented: Petalosoma infections appear at 23.0 °C-27.4 °C, while Cryptocaryon and Benedenia outbreaks are linked to late-summer temperatures around 27 °C-28.8 °C and become especially serious at 28.2 °C-28.5 °C.

4.2 Changes in immune-related enzyme activities and inflammatory responses

Multiple stressors related to intensive culture can mimic or interact with high-temperature stress by activating antioxidant and immune enzymes. Under long-term high stocking density, large yellow croaker show elevated liver SOD and CAT activities and increased HSP70/HSP90 and glutathione S-transferase gene expression, indicating chronic oxidative and cellular stress (Yu et al., 2024). During parasitic *Metanophrys* sp. infection, tissue- and time-specific shifts in SOD, CAT, MDA, lysozyme, and Na⁺/K⁺-ATPase activities in skin, gill, and liver reflect increased oxidative stress and activation of mucosal defenses over 0-72 h post-infection (Zhou et al., 2025).

Inflammatory signaling is strongly remodeled under infection and stress. *Aeromonas hydrophila* infection drives large changes in splenic transcriptomes, with many differentially expressed genes in Toll-like receptor, JAK-STAT, and MAPK pathways and marked shifts in inflammatory genes, highlighting a central role of inflammatory responses early in infection. At the cellular level, regulators such as Trim38 and farnesoid X receptor (FXR) modulate NF-κB-driven cytokine production and ER-stress-linked inflammation, suggesting that controlling these pathways can limit tissue damage during intense or prolonged inflammatory activation.

4.3 Mechanisms of gut microbiota dysbiosis

Pseudomonas plecoglossicida infection in large yellow croaker illustrates how disease and temperature-relevant stress can reshape gut communities and immunity. The pathogen colonizes the gut, elevates mortality, induces persistent up-regulation of pro-inflammatory cytokines (TNF-α1, TNF-α2, IL-1β) and IL-10, and triggers only transient increases in non-specific immune enzymes at early stages (Li et al., 2020). This infection leads to irreversible disruption of the gut microbiota, with infection status explaining a substantial fraction of community variation; dysbiosis is statistically linked to immune activity and is proposed as a direct cause of rising mortality.

Findings from other fish support common mechanisms by which heat stress drives dysbiosis and barrier damage, which are likely relevant to large yellow croaker in warm seasons. In rainbow trout exposed to acute heat stress, rising temperatures reduce gut microbial diversity, shift community composition, and are tightly associated with altered serum metabolites (amino acids, vitamins, short-chain fatty acids); concurrent damage to intestinal structure, barrier integrity, antioxidant capacity, and increased pro-inflammatory cytokines indicates that microbiota changes and metabolic dysfunction jointly mediate heat-induced intestinal injury. Similarly, high-temperature exposure in rainbow trout disrupts epithelial and goblet cells, increases IL-1β and IL-8 expression, and alters microbiota composition and KEGG pathways related to immune function, underscoring the tight crosstalk between gut immunity and microbiota under thermal stress (Zhao et al., 2023).

5 Environmental Regulation Strategies in Aquaculture Systems

5.1 Water temperature control and stratification management techniques

Fish in thermally variable coastal systems naturally adjust depth and habitat to remain near preferred temperatures, moving deeper during warm summers and shifting as stratification reverses in winter. This behavior indicates that

aquaculture systems for large yellow croaker should minimize sharp temperature gradients and provide access to thermally suitable layers, especially during peak summer surface warming. Reviews on extreme temperature events in aquaculture suggest that structural modifications such as increased water depth or coverings, and the use of recirculating systems, can buffer fish from temperature spikes (Islam et al., 2021).

Experimental work on recirculating ponds shows that optimizing the layout, perforation rate, and angles of water supply pipelines can markedly improve thermal uniformity and weaken stratification (Zhang et al., 2024). In larger water bodies, selective withdrawal strategies that adjust intake depth can raise downstream water temperatures during critical spawning and growth periods while weakening reservoir stratification, offering a model for managing inflow and outflow depths in large pond or reservoir-based aquaculture (Wang et al., 2024).

5.2 Dissolved oxygen optimization and water circulation system design

In feed-based ponds, major oxygen sources are phytoplankton photosynthesis and mechanical aeration, while fish and microbial respiration constitute dominant sinks, leading to high daytime oxygen but dangerously low nighttime levels under warm, eutrophic conditions. Reviews of aeration technologies emphasize that selecting efficient aerators and correctly sizing and positioning them is crucial to maintain optimal dissolved oxygen in intensive systems.

Empirical studies in brackish ponds demonstrate that paddle-wheel aerator placement, as well as seasonal variation in total dissolved and suspended solids, strongly influence mixing intensity, water velocities, and oxygen transfer rates, and that data-driven models can forecast dissolved oxygen with high accuracy to guide aeration scheduling (Ramesh et al., 2024). In RAS, simple pipeline diffused aeration systems using pure oxygen have been shown to substantially increase outlet dissolved oxygen with predictable performance based on pipe length, inlet oxygen, and contact time, allowing controllable DO regulation during periods of high temperature and metabolic demand (Ji et al., 2024).

5.3 Water quality regulation and pollutant control strategies

Dynamic modeling of RAS highlights that ammonia, nitrite, nitrate, dissolved oxygen, and pH are tightly linked to fish metabolism, feeding intensity, biofilter performance, and water exchange, and that strengthening biological filtration and oxygenation is key to preventing toxic accumulations (Udayakumar et al., 2025). Reviews of recirculating systems detail that particulate matter, nitrogen pollutants, phosphate, carbon dioxide, antibiotics, steroids, and heavy metals can build up and compromise fish health, so integrated treatment units must filter or degrade these substances and recycle purified water (Li et al., 2023).

Biological approaches have been particularly effective for nitrogen control. Bacteria-microalgae associations in recirculating ponds significantly reduced total nitrogen, ammonia, and nitrite while improving fish production, supported by shifts in microbial communities toward nitrification and denitrification pathways. Similarly, assembled bacterial consortia of *Bacillus* and *Pseudomonas* species have efficiently converted ammonia to nitrite and further to less toxic nitrate in aquaculture wastewater, greatly improving fish survival compared with untreated controls. Reviews focused on *Bacillus* species confirm their broad capacity to modulate physical and chemical water quality parameters, including nitrogenous species, heavy metals, and microbial balance, offering a cost-effective tool for maintaining stable environments during stressful warm periods (Figure 2).

6 Nutritional and Feeding Management Strategies

6.1 Adjustments of energy and protein requirements under high temperature

High summer temperatures increase metabolic costs, so diets must supply sufficient digestible energy while avoiding excessive metabolic and oxidative burden. Recent reassessment of large yellow croaker nutrition in net pens indicates that crude protein levels of about 490-520 g/kg combined with 90 g/kg lipid support fast growth, high nitrogen retention, and appropriate body lipid with normal antioxidant capacity, suggesting this range as a baseline for high-demand periods (Chen et al., 2023). For thermal stress conditions, evidence from spotted seabass shows that protein requirements can shift with temperature, with slightly lower optimal protein at 33 °C than at 27 °C, indicating that heat alters nutrient metabolism and the efficiency of protein use.

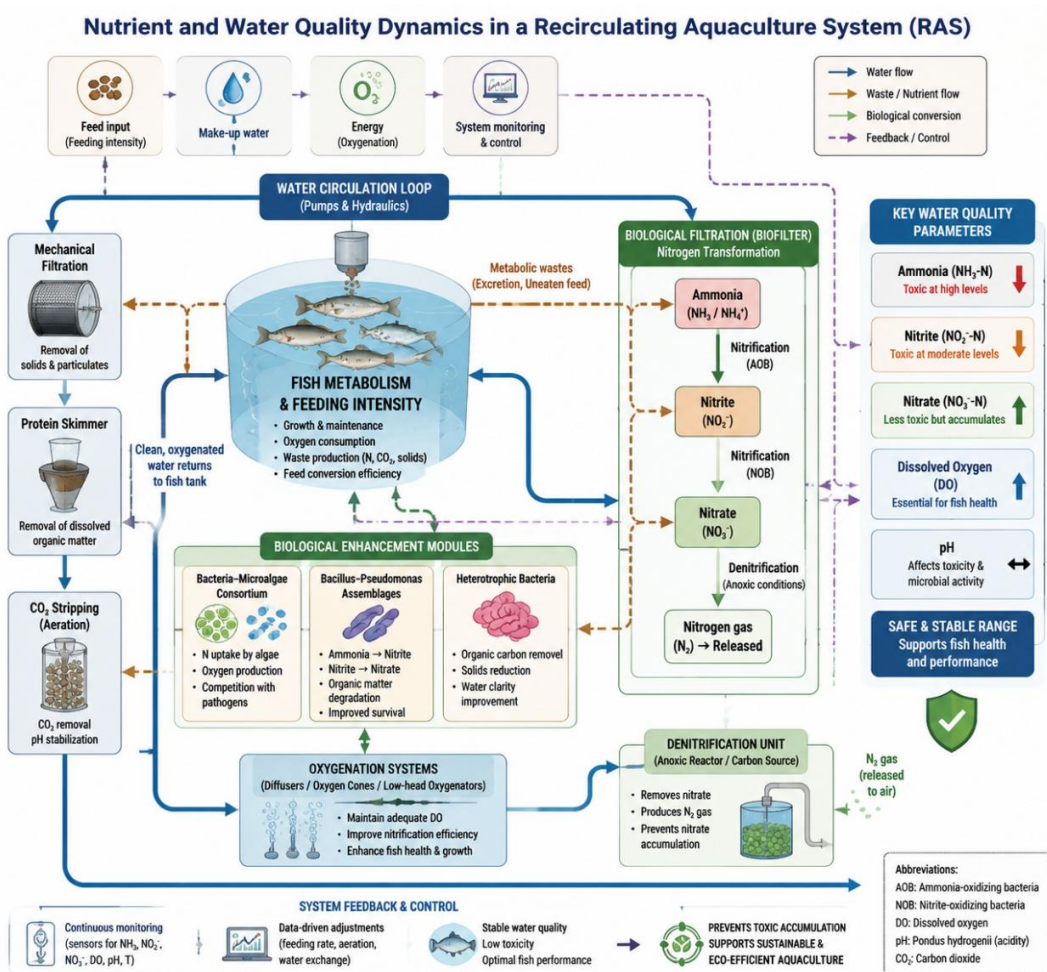


Figure 2 Systems-level interactions in recirculating aquaculture systems (RAS), illustrating feedback loops between fish metabolism, nitrogen cycling processes, and biological treatment units including nitrifying bacteria, bacterial consortia, and microalgae

Balancing protein with non-protein energy is critical to spare protein for growth and limit catabolic stress under high temperature. In large yellow croaker, elevating dietary lipid from 60 to 90 g/kg improves weight gain and nitrogen retention, but further increase to 120 g/kg does not enhance performance, implying an upper threshold for effective energy supplementation (Chen et al., 2023). The same study estimates a suitable dietary energy content around 19 MJ/kg and notes that when energy needs are satisfied, additional lipid no longer induces protein-sparing, which is important when setting rations during hot seasons.

6.2 Functional feed additives

Under high-temperature, high-density culture, functional additives that stabilize immunity and gut health become key complements to macronutrient adjustments. Broad aquaculture evidence shows that bio-friendly supplements such as probiotics, prebiotics and synbiotics can improve growth and stress mitigation while modulating intestinal microbiota and immune competence, thereby reducing reliance on antibiotics. Reviews on aquaculture feed additives further emphasize that immunostimulants (e.g., β -glucans, nucleotides) and prebiotics regulate innate defenses and gut barrier function, with typical inclusion ranges of a few g/kg diet (Okon et al., 2025).

For large yellow croaker specifically under summer heat stress, dietary inulin has emerged as a promising prebiotic strategy. A two-month trial across July-September showed that an inulin level around 0.4% significantly improved growth, accompanied by up-regulation of glycolysis and fatty-acid biosynthesis genes and increased metabolites supporting energy production. Inulin also reshaped the gut microbiota with enrichment of beneficial bacteria such as *Lactobacillus* and higher levels of short-chain fatty acids and amino acids, suggesting enhanced nutrient absorption and thermal stress tolerance (Yin et al., 2026).

6.3 Optimization of feeding strategies and regulation of feeding behavior

Feeding strategy must adapt to the combined effects of temperature, water quality, and fish appetite to avoid over- or under-feeding during hot periods. Under experimentally imposed high-temperature stress in common carp, an intermittent strategy of feeding every third day produced higher weight gain, better specific growth rate, lower feed conversion ratio, and enhanced digestive enzyme activities compared with daily feeding, while also improving antioxidant status. Behavioral analysis in *Pangasius* culture cages likewise shows that optimal feeding rates depend on weather-driven changes in temperature, pH, and dissolved oxygen, with higher intake feasible on warm, sunny days but reduced rations recommended during cloudy or rainy conditions to avoid waste and water quality deterioration (Yashashvi et al., 2023).

Technological tools for monitoring and regulating feeding behavior can further refine summer feeding management. Reviews of intelligent feeding control highlight that traditional fixed schedules often fail to match dynamic appetite and can lead to excessive or insufficient feeding, whereas behavior-based automatic systems use models, acoustic sensing, or computer vision to determine real-time demand. A complementary line of work on automatic recognition of feeding behavior shows that many methods can quantify feeding intensity, but accuracy in complex environments still needs improvement, pointing to the potential of data fusion and deep learning for precise control under fluctuating summer conditions (Li et al., 2020).

7 Case Study: Practical Health Management of Large Yellow Croaker under High-Temperature Conditions

7.1 Typical high-temperature aquaculture regions and system setup

Large yellow croaker farming is concentrated in warm, shallow coastal waters of southeastern China, where cage culture has become the dominant production mode and main source of national mariculture output. Typical cage-culture districts in Fujian such as Jiaocheng, Shacheng and Xiapu show regional differences in growth performance, with Xiapu fish achieving the highest asymptotic size and weight, suggesting that local hydrology and thermal regimes strongly affect production efficiency (Chen et al., 2020).

Summer sea surface temperatures in these regions increasingly approach 30 °C, narrowing thermal safety margins and challenging traditional floating cage systems that are shallow and restrict behavioural thermoregulation (Figure 3). Review work on large yellow croaker aquaculture highlights that floating sea-cages remain the main farming model, but deep-sea cages and indoor recirculating systems are being promoted to better simulate natural habitats and buffer environmental extremes, providing alternative setups for high-temperature seasons (Thanhhoa et al., 2020).

7.2 Application effects of integrated management measures

Case comparisons between nearshore cages and a mobile offshore aquaculture ship demonstrate how integrated environmental management directly improves health outcomes during warm months. The ship system maintained water temperatures mostly within 21.5 °C-28.5 °C and dissolved oxygen of 7.2-12.8 mg/L, with low ammonia and relatively low bacterial and *Vibrio* counts, and achieved 99.02 % survival and markedly higher growth than cages. By contrast, nearshore cages experienced prolonged high temperature and chronically low dissolved oxygen, conditions linked to oxidative stress, impaired digestion and immunity, and higher mortality, underlining the value of mobile or deeper systems that can track optimal water masses (Yu et al., 2023).

Nutritional and stock-management measures complement environmental control in mitigating heat stress. Long-term high stocking density elevates cortisol, antioxidant and stress-related enzymes, while depressing immune parameters, and authors recommend controlling final density to 14.41-18.71 kg/m³ in intensive systems to preserve health and product quality (Yu et al., 2024). During summer heat, targeted functional feeds such as inulin or fulvic acid have significantly improved growth, survival and thermal resilience, partly by enhancing energy metabolism pathways and beneficial gut microbiota, indicating that nutrition can offset some high-temperature pressures when integrated with environmental and density management.

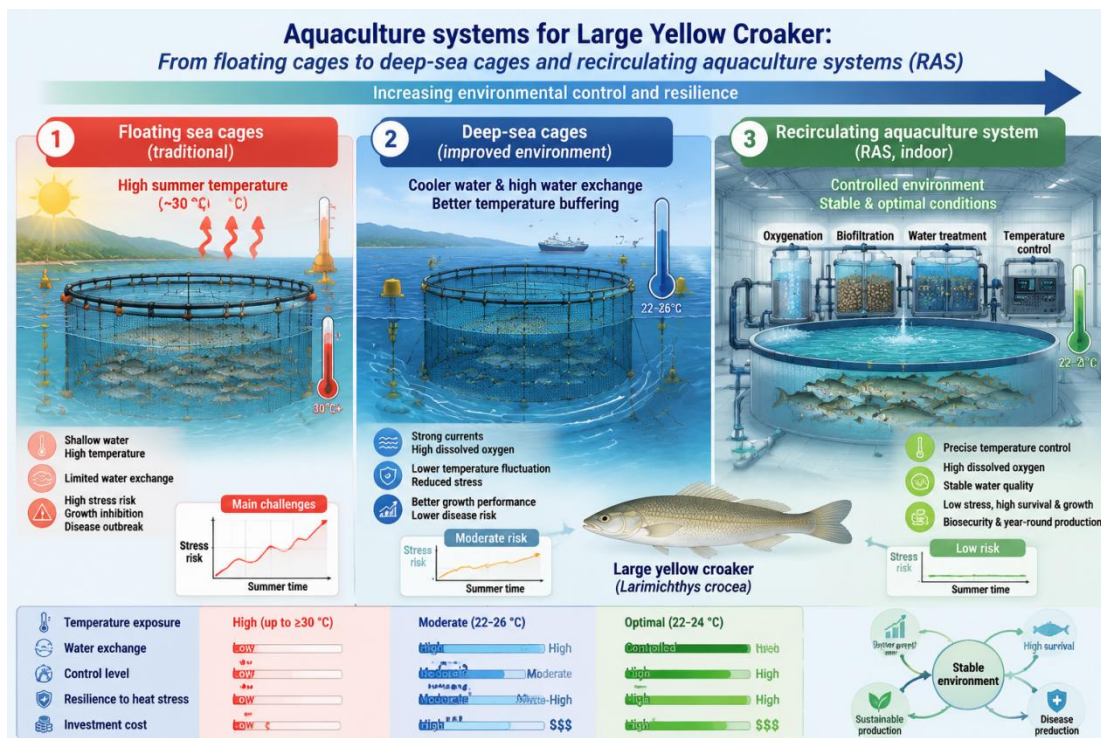


Figure 3 Comparison of farming systems for large yellow croaker, illustrating traditional floating cages, deep-sea cages, and recirculating aquaculture systems (RAS) as adaptive responses to environmental stress

7.3 Comparative analysis of success and failure cases and experience summary

Comparisons across culture modes and regions reveal clear patterns distinguishing successful high-temperature management from failure. Offshore ship aquaculture, operating within moderate temperature and high oxygen ranges and maintaining low nitrogen and bacterial levels, achieved near-complete survival and superior flesh composition, whereas static nearshore cages exposed to heat and hypoxia suffered slower growth and higher mortality, illustrating the cost of inadequate environmental buffering. Regionally, heavily eutrophic areas with low pH and dissolved oxygen, such as one major cage region where nutrients and heavy metals were highest, present higher ecological risk and poorer fish quality than better-managed sites, emphasizing that pollution control is integral to heat-season health management (Chen et al., 2025).

Experience from thermal biology and breeding research further refines these practical lessons. Large yellow croaker show appreciable thermal plasticity and high formal thermal safety margins, yet prolonged exposure to 30 °C still causes energy reallocation, growth depression and oxidative stress, warning against relying solely on nominal tolerance when designing summer strategies. At the same time, genetic and seed selection work stresses the need to integrate traits such as disease resistance and environmental stress adaptation into breeding and to pair improved strains with intelligent environmental control, precision feeding and disease prevention, forming a comprehensive package for robust performance under future hotter summers.

8 Health Monitoring and Early Warning Technologies

8.1 Physiological indicators and behavioral monitoring techniques

High-temperature seasons demand noninvasive techniques that track physiological stress in large yellow croaker without adding further injury risk. A high-temperature stress study showed that cortisol in serum, skin mucus, and surrounding water followed a similar “rise then fall” pattern, peaking at 1.5 h, and that cortisol levels in these three media were highly correlated, supporting skin mucus and tank water as practical substitutes for blood sampling. Parallel measurement of MDA, IgM, and AKP in serum and skin mucus further indicates that oxidative damage and immune status can also be followed through mucus, enabling repeated monitoring during heatwaves without sacrificing fish.

Behavioral responsiveness provides another early window into stress before overt disease emerges. In large yellow croaker subjected to a brief net-restraint challenge, consistent differences in recovery latency and exploration activity revealed proactive and reactive coping styles, with faster-recovering fish showing lower plasma cortisol and higher IgM at 7 days after stress (Li et al., 2024). Hypoxia studies show that restlessness, constant floating, and increased respiratory rate are accompanied by up-regulation of muscular movement and energy-generation genes, linking observable behavior with defined molecular pathways, which could be exploited for automated video-based stress surveillance during warm, low-oxygen nights (Chen et al., 2024).

8.2 Molecular biology and pathogen detection methods

Rapid pathogen diagnosis is essential because co-infections and temperature fluctuations can drive sudden mortalities in marine farms. A broad review of bacterial fish diseases emphasizes that molecular assays such as conventional PCR, real-time PCR, multiplex PCR, LAMP, microarrays, and sequencing provide faster and more sensitive identification of septicemic agents than traditional culture, supporting early intervention and targeted antimicrobial use. These tools also allow monitoring of pathogen abundance in asymptomatic carriers and the environment throughout the production cycle, which is critical for preventive health management under stressful summer conditions (Abdelsalam et al., 2022).

For large yellow croaker specifically, a duplex PCR assay targeting *ompA* genes of *Klebsiella pneumoniae* and *Chryseobacterium* enables simultaneous detection and discrimination of these emerging pathogens, which often produce similar clinical signs (Hu et al., 2024). The method detects as little as 20-200 fg genomic DNA or about 100 CFU, correctly identifies single and mixed infections in field samples, and is described as time-saving, specific, and convenient for epidemiological surveillance in aquaculture.

8.3 Construction of intelligent aquaculture and early warning systems

Modern disease control increasingly relies on integrated sensor and data-analytics platforms. Reviews of cutting-edge fish disease technologies highlight that IoT sensors, artificial intelligence, and machine-learning models can continuously track environmental parameters and fish activity, allowing farmers to predict disease outbreaks and intervene before large mortality occurs. Image-based systems using 2D/3D cameras under near-infrared light can capture swimming patterns and skin changes to detect early behavioral or external lesions, demonstrating practical noninvasive monitoring that can be embedded into early-warning workflows (Islam et al., 2024).

At the system level, IoT-ML architectures have proven capable of stabilizing water quality and reducing mortality in tropical aquaculture, even during high-temperature periods. One implementation using low-cost sensors to monitor temperature, dissolved oxygen, pH, and turbidity achieved extremely high predictive accuracy for water-quality parameters and enabled over 6000 automated corrective interventions, maintaining fish survival above 90% (Baena-Navarro et al., 2025). Complementary AIIoT reviews describe how networks of sensors and cameras feeding AI models can jointly support water-quality prediction, disease recognition, and smart feeding, forming the backbone of intelligent aquaculture farms that can issue timely alerts and automate responses under rapidly changing thermal conditions.

9 Conclusions and Prospects

High-temperature seasons pose a central constraint on large yellow croaker aquaculture by narrowing the thermal safety window, redistributing energy away from growth, and increasing the risk of oxidative stress, hypoxia, and disease. Across systems, maintaining water temperature within the species' optimal range, ensuring sufficient dissolved oxygen, and avoiding sharp daily fluctuations emerged as the core environmental requirements for sustaining performance during summer. At the same time, evidence from ship-based offshore systems and improved cage designs shows that environmental risks can be substantially reduced through better site selection, mobility, and stratification management. Nutritional and health management strategies can further buffer thermal stress. Optimized protein-energy ratios, together with functional additives such as inulin and fulvic acid, support growth, stabilize metabolism, and reshape gut microbiota in favour of beneficial taxa under high summer temperatures.

Integrated multi-omics studies indicate that these diets enhance energy pathways while down-modulating excessive stress and inflammatory responses. In parallel, emerging breeding work on heat-tolerant and stress-resistant lines, along with gradually adopted intelligent monitoring and AI-supported decision tools, suggests that biological, nutritional, and technological approaches can be combined into a coherent health management framework for hot seasons.

Despite rapid progress, most experimental studies on large yellow croaker thermal stress are short-term, carried out under controlled or semi-controlled conditions, and focus on single factors such as temperature, diet, or transport. This limits understanding of how chronic multi-stressors—heat combined with hypoxia, pollutants, high density, and pathogens—interact over full production cycles. In addition, many multi-omics investigations are done at juvenile stages and in specific seasons, creating uncertainty about how findings scale to different life stages, strains, and farming regions. Methodologically, current work is often fragmented between physiology, nutrition, genetics, and engineering. Large, integrative field trials that compare different culture systems, diets, and management packages under realistic summer conditions remain scarce. Meanwhile, smart aquaculture and AI/AIoT research is dominated by generic models and laboratory or pilot demonstrations, with relatively few tools tailored to the behaviour, color, schooling patterns, and disease spectrum of large yellow croaker. Barriers such as high initial costs, requirement for technical expertise, and lack of standardized data pipelines also slow real-world deployment.

Future research should prioritize long-term, system-level studies that couple environmental regulation (temperature, oxygen, water quality) with precision nutrition, stocking-density control, and disease prevention for entire summer grow-out cycles. Combining multi-omics with continuous environmental and behaviour monitoring can clarify how specific management packages influence resilience, growth, and product quality. Parallel breeding and genomic selection programs targeting acute and chronic heat tolerance, hypoxia resistance, and disease robustness will be critical to create strains adapted to future warming. On the technological side, intelligent fish-farm concepts and AIoT platforms offer powerful prospects for high-temperature health management. Networked sensors, computer vision, and machine-learning models can underpin real-time control of feeding, aeration, and environmental alarms, while advanced diagnostic tools and AI-based disease recognition can support earlier, more targeted interventions. To make these solutions practical for croaker farmers, future work should emphasize species-specific model training, cost-effective modular hardware, explainable interfaces, and capacity building. Ultimately, integrating heat-tolerant germplasm, functional feeds, optimized offshore or recirculating systems, and intelligent management tools will be the key pathway to resilient, sustainable large yellow croaker aquaculture under a warming climate.

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Conflict of Interest Disclosure

The author affirms that this research was conducted without any commercial or financial relationships that could be construed as a potential conflict of interest.

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Review Article

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Evaluation of Sea Cucumber Growth Under Different Stocking Densities

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Abstract Sea cucumber aquaculture has become an important sector of the marine farming industry due to the high nutritional and economic value of sea cucumbers. Among the various management practices, stocking density is recognized as one of the most critical factors affecting growth performance, survival, resource utilization, and production efficiency. This paper evaluates the effects of different stocking densities on sea cucumber growth by reviewing the biological characteristics of sea cucumbers, key factors influencing density determination, growth assessment indicators, and the physiological and ecological mechanisms associated with density-dependent responses. Particular attention is given to the interactions among stocking density, feeding behavior, environmental quality, and competitive pressure. The analysis indicates that moderate stocking densities generally promote optimal growth, higher survival rates, and efficient utilization of available resources, whereas excessively high densities may result in increased competition, environmental deterioration, physiological stress, and reduced growth performance. Conversely, excessively low densities may lead to underutilization of culture facilities and decreased production efficiency. A case study of practical sea cucumber farming further demonstrates the importance of density optimization in balancing economic returns and ecological sustainability. The findings highlight the necessity of adopting scientifically determined stocking densities according to culture conditions, developmental stages, and management objectives. This study provides a theoretical basis and practical guidance for improving sea cucumber culture productivity and supporting the sustainable development of the sea cucumber aquaculture industry.

Keywords Sea cucumber; Stocking density; Growth performance; Aquaculture management; Culture sustainability

1 Introduction

Sea cucumbers are high-value invertebrates increasingly farmed to meet growing demand and to reduce pressure on overexploited wild stocks. Aquaculture has become an established industry in parts of Asia, especially China, where large-scale production of *Apostichopus japonicus* and other species now supplies most domestic consumption and supports stock enhancement and ocean ranching initiatives. At the same time, serial overexploitation of global fisheries and sharp declines in wild populations have prompted interest in aquaculture, ranching, and restocking as tools for both production and conservation. In emerging regions such as the Mediterranean and North-East Atlantic, aquaculture is still developing, but is viewed as essential for relieving harvesting pressure and restoring depleted stocks. Stocking density is a central variable in sea cucumber culture because it directly affects growth, survival, physiology, and welfare. Many studies report that growth performance generally declines as density increases, with low to moderate biomasses yielding higher individual growth and high densities often causing growth depression or even negative growth (Ciriminna et al., 2024). Experiments with *Holothuria scabra* and *Holothuria atra* show that low stocking densities in pens or cages produce greater weight gain per individual than higher densities, while survival may remain acceptable across a range of densities (Hartati et al., 2020).

Beyond effects on growth, high densities can act as a chronic stressor, altering behavior, digestion, and stress physiology, and may reduce disease resistance and tolerance to additional stressors in *A. japonicus* (Tian et al., 2024; Tian et al., 2025). Optimal stocking density has implications not only for animal performance but also for ecosystem processes and the environmental footprint of farms. As deposit-feeders and ecosystem engineers, sea cucumbers ingest large amounts of sediment, enhancing nutrient cycling, modulating dissolved oxygen and nutrient levels, and influencing organic matter dynamics in benthic systems. In integrated multitrophic aquaculture, increasing sea cucumber biomass can improve bioremediation of particulate waste and, at moderate densities, reduce sediment

organic loading and enhance water quality, but exceeding critical densities may compromise growth yield and alter carbon and nitrogen fluxes (Mei et al., 2022). Modeling work indicates that bioremediation benefits in IMTA are constrained by limits to stocking density, as growth decreases or stops beyond critical biomass levels due to competition for space and food. (Chary et al., 2020). Building on this background, the present study, titled “Evaluation of Sea Cucumber Growth Under Different Stocking Densities,” aims to quantify how a defined range of densities affects growth performance and survival under controlled culture conditions. Previous work shows that juvenile and grow-out stages of *H. scabra* and *A. japonicus* exhibit density-dependent growth responses, with specific growth rate and final body weight often declining at higher densities, yet optimal thresholds remain species- and system-specific. This study therefore asks how do different stocking densities influence growth rate, survival, and size variability; and is there an intermediate density that maximizes biomass yield without inducing strong stress responses? Based on prior evidence that low to moderate densities enhance individual growth while very high densities reduce growth and can trigger physiological stress, the working hypothesis is that sea cucumber growth will be highest at intermediate stocking densities, with both lower and higher densities yielding reduced performance (Chary et al., 2020).

Sea cucumber aquaculture is expanding to meet demand and relieve pressure on overfished wild stocks, making efficient and sustainable grow-out practices critical. Evidence from multiple species indicates that stocking density strongly affects growth, survival, physiology, and environmental interactions, with low to moderate densities generally performing best. The planned study will test density-growth relationships in a defined system, with the expectation that intermediate densities will optimize growth while maintaining acceptable welfare and environmental conditions.

2 Literature Review

2.1 Research progress on major sea cucumber culture models and environmental adaptability

Sea cucumber aquaculture has expanded rapidly in China and the tropics, supported by hatchery production and diversified grow-out systems including earthen ponds, dedicated ponds and ocean ranching for *Apostichopus japonicus* and *Holothuria scabra*. Across regions, culture models include hatchery-pond grow-out, sea pens, bottom sea ranching and integrated multi-trophic aquaculture (IMTA), each with distinct constraints on density, food supply and environmental loading (Chary et al., 2020). In Europe and the NE Atlantic, sea cucumber aquaculture is still emergent, with fragmented knowledge on species biology, early life stages and optimal rearing conditions limiting full-cycle farming. Environmental adaptability varies strongly among species in IMTA: some, like *Holothuria poli*, show reduced growth under waste-enriched conditions, whereas others tolerate or benefit from co-culture, emphasizing the need to match species’ natural feeding strategies and sediment niches to specific farming systems (Ciriminna et al., 2024).

2.2 Mechanisms by which density stress affects the growth of benthic marine invertebrates

Experimental work with *A. japonicus* shows that high stocking density alters behavior, suppressing feeding over longer periods and modifying neurochemical regulation (elevated GABA), which likely reallocates energy away from growth toward coping with crowding (Tian et al., 2024). Under additional stressors such as bacterial challenge or acute temperature drop, high density elevates morbidity and further depresses righting and feeding responses, suggesting reduced stress resistance mediated by changes in antioxidant and metabolic enzymes (e.g., SOD, pyruvate kinase). Moderate densities can enhance metabolic activity and growth, whereas excessive crowding leads to energy diversion into homeostasis and competition, reducing growth efficiency. (Mei et al., 2022) Similar patterns are inferred for other benthic invertebrates in IMTA, where too low sea cucumber density limits bioremediation, but too high densities compromise survival, feeding and output, underscoring density as a chronic stressor linked to food competition, waste accumulation and water-quality deterioration (Chary et al., 2020; Onomu et al., 2024).

2.3 Current status and limitations of domestic and international research on sea cucumber density optimization

Across culture systems, many studies report higher individual growth at low or moderate densities and growth depression at high densities, but the “optimal” level is highly system- and species-specific (Hartati et al., 2020). For

H. scabra and *A. japonicus*, net-cage and pond studies suggest recommended juvenile stocking around 80-90 g/m² or moderate biomass levels, with suppressed growth and sometimes increased mortality when densities exceed empirically derived thresholds. However, current density-optimization research is fragmented: many experiments use different size classes, weight metrics and feeding regimes, limiting cross-study comparability and meta-analysis (Ciriminna et al., 2024). Moreover, most work focuses on short-term growth and survival rather than integrating density with bioremediation goals, economic performance and welfare, even though modeling studies show that optimal densities for growth may not coincide with those maximizing waste removal in IMTA (Chary et al., 2020; Ren et al., 2024).

3 Key Factors Determining Stocking Density in Sea Cucumber Culture

3.1 Sea cucumber growth stages and requirements for optimal stocking density

Stocking density must be matched to the life stage of sea cucumbers because growth responses to crowding differ markedly between larvae, juveniles, and adults. Studies on auricularia larvae of *Parastichopus californicus* show that specific growth rate and metamorphosis decline sharply at high larval densities, with optimal performance at or below 0.5 larvae/mL, highlighting the sensitivity of early stages to density-dependent competition for microalgal feed. For nursery phases, juvenile *Holothuria scabra* reared in tanks can achieve very high specific growth rates when provided with appropriate algal diets, but survival and growth still depend on keeping biomass within limits that do not compromise water quality or feed availability (Campo et al., 2022). During grow-out, density-growth relationships are strongly size-dependent, with smaller juveniles often tolerating higher areal densities than larger conspecifics. In *Holothuria tubulosa*, juveniles (~40 g) stocked at 6 ind/m² had markedly higher weight gain and specific growth rate than those at 15 or 30 ind/m², where growth became negligible or negative, indicating a clear optimal density threshold for this size class. Similarly, in *Apostichopus japonicus*, smaller individuals showed higher specific growth rates than medium and large conspecifics across densities, implying that optimal biomass must be periodically adjusted as animals grow to prevent density-induced growth depression and survival losses at high total biomass (e.g., 850 g/m²).

3.2 Influence of culture environmental conditions on density settings

Environmental conditions modulate the density that a given life stage can tolerate, particularly through effects on food supply, sediment quality, and water quality. In integrated mariculture of *Holothuria scabra* with *Eucheuma denticulatum*, low sea cucumber densities produced the highest individual growth rate, while medium densities most effectively reduced sediment total organic matter and carbon, indicating that both growth and bioremediation outcomes depend on interactions between density and organic loading. Similarly, in sea ranching of *Holothuria atra*, stocking time and the development of microphytobenthos on the cage sediments influenced growth, with the second stocking period yielding the highest weight gain at low density, showing how benthic food resources and rearing duration shape effective density limits (Hartati et al., 2020). Water temperature, substrate type, and system design also constrain stocking density. A dynamic energy budget model for *Apostichopus japonicus* emphasized the importance of accurate lower and upper thermal tolerance boundaries because hibernation and aestivation periods create fast-growth and non-growth phases that alter how much biomass a pond or co-culture system can support at different seasons. In land-based IMTA tanks, negative growth of *Neostichopus grammatus* across densities was attributed not to biomass but likely to bare-bottom tanks without sand substrate, underscoring that unsuitable habitat structure can effectively lower the carrying capacity and make even moderate densities unsustainable (Onomu et al., 2024).

3.3 Regulation of carrying capacity by culture models and management measures

Different culture models-ponds, pens, cages, and open-water IMTA-have distinct physical and trophic constraints that define carrying capacity and thus acceptable stocking densities. Modeling work for *Parastichopus californicus* in IMTA systems showed that deposit feeders can substantially reduce particulate organic carbon loading (up to 86%-99%) and strongly enhance their own production beneath finfish and shellfish cages, but only when densities are set within ranges that balance waste supply and benthic assimilation. In field IMTA trials with *Holothuria poli* near Mediterranean fish cages, mass mortalities directly under cages highlighted that exceeding local ecological

carrying capacity via high biodeposit flux and suboptimal cage setup can negate growth despite adequate food, emphasizing the need to integrate hydrodynamic and deposition patterns into density decisions (Cutajar et al., 2022; Sadoul et al., 2022). Within each model, management measures such as feeding regime, cleaning frequency, and staged stocking adjust the effective carrying capacity over time. In intensive culture of *Holothuria scabra*, high-quality diets can partially offset density-related growth limitations by improving feed conversion and protein efficiency, but crowding still affects survival, health, and feeding, indicating that management can shift but not eliminate density thresholds. In ranching of *Holothuria atra*, repeated stocking events and monitoring of sediment pigments allowed managers to time low-density stockings to periods when microphytobenthos had recovered, thereby improving growth while maintaining acceptable survival at higher densities, demonstrating how adaptive stocking schedules and habitat monitoring can dynamically regulate carrying capacity in open systems (Hartati et al., 2020).

4 Growth Performance Indicators and Statistical Analysis

4.1 Construction of growth indicator systems (weight gain rate, specific growth rate, survival rate, etc.)

In density and feeding experiments on sea cucumbers and other aquaculture species, growth performance is typically quantified through a set of complementary indicators that capture both absolute and relative changes in body mass and population status. For juvenile *Holothuria tubulosa*, growth was monitored by wet weight and summarized using weight gain (WG), growth rate (GR), specific growth rate (SGR), relative weight gain (RWG), coefficient of variation (CV), and survival rate (SR) over the rearing period. Similar indicator suites have been applied for *Holothuria poli* in long-term integrated multi-trophic aquaculture, where relative weight gain, growth rate, SGR and survival rate were calculated from initial and final wet weights and numbers per cage. These indicators are derived from standardized formulas that facilitate comparison across treatments and studies. For *H. poli*, RWG is defined as $100 \times (W_2 - W_1) / W_1$, GR as $(W_2 - W_1) / t$, SGR as $100 \times (\ln W_2 - \ln W_1) / t$, and SR as $100 \times (n_2 / n_1)$, using initial and final mean wet weight (W_1 , W_2), culture duration (t), and animal numbers (n_1 , n_2) (Cutajar et al., 2022). In sea cucumber density trials, these metrics have been sensitive to stocking density, with SGR, RWG and SR often declining at higher densities, underscoring their suitability as core indicators for evaluating growth responses to crowding.

4.2 Measurement methods for feeding efficiency and energy utilization indicators

Feeding efficiency in sea cucumbers is commonly evaluated through food conversion efficiency (FCE), protein efficiency ratio (PER), apparent digestibility coefficients (ADCs) and related energy budget components. In a 60-day study on *Apostichopus japonicus*, diets with graded biofloc levels significantly affected SGR, FCE and PER, and allowed estimation of optimal dietary replacement levels using polynomial regression of SGR and FCE. Energy allocation was expressed using a full budget (e.g., $100C = 3.8G + 65.4F + 3.3U + 27.5R$), partitioning ingested energy (C) into growth, feces, excretion and respiration, which revealed how diet altered the balance between growth deposition and metabolic losses. Under combined feeding-frequency and density manipulation, energy budget indicators were further linked to crowding stress. In *A. japonicus*, feed intake, energy intake and feces production rate were significantly affected by both feeding frequency and stocking density, and high density reduced food conversion efficiency and protein efficiency ratio while decreasing apparent digestibility of crude protein and lipid. The same study quantified how crowding shifted energy allocation, with energy for growth decreasing and metabolic energy increasing as density rose, supported by endocrine indicators such as elevated cortisol and lactate.

4.3 Statistical analysis methods (ANOVA, multiple comparisons, and regression analysis)

Analyses of density effects on growth indicators in sea cucumbers and other cultured species rely heavily on ANOVA and multiple comparison procedures to test for treatment differences. For *Holothuria scabra*, two-way ANOVA was used to evaluate the effects of feeding regime and stocking density on total and monthly weight gain, with one-way ANOVA applied to daily weight gain and SGR; significance was set at $P < 0.05$ (Figure 1). Similar designs are widely used in density-growth studies of fish and invertebrates, typically followed by Tukey's or Duncan's multiple range tests to identify which stocking densities differ in growth, feed conversion or survival.

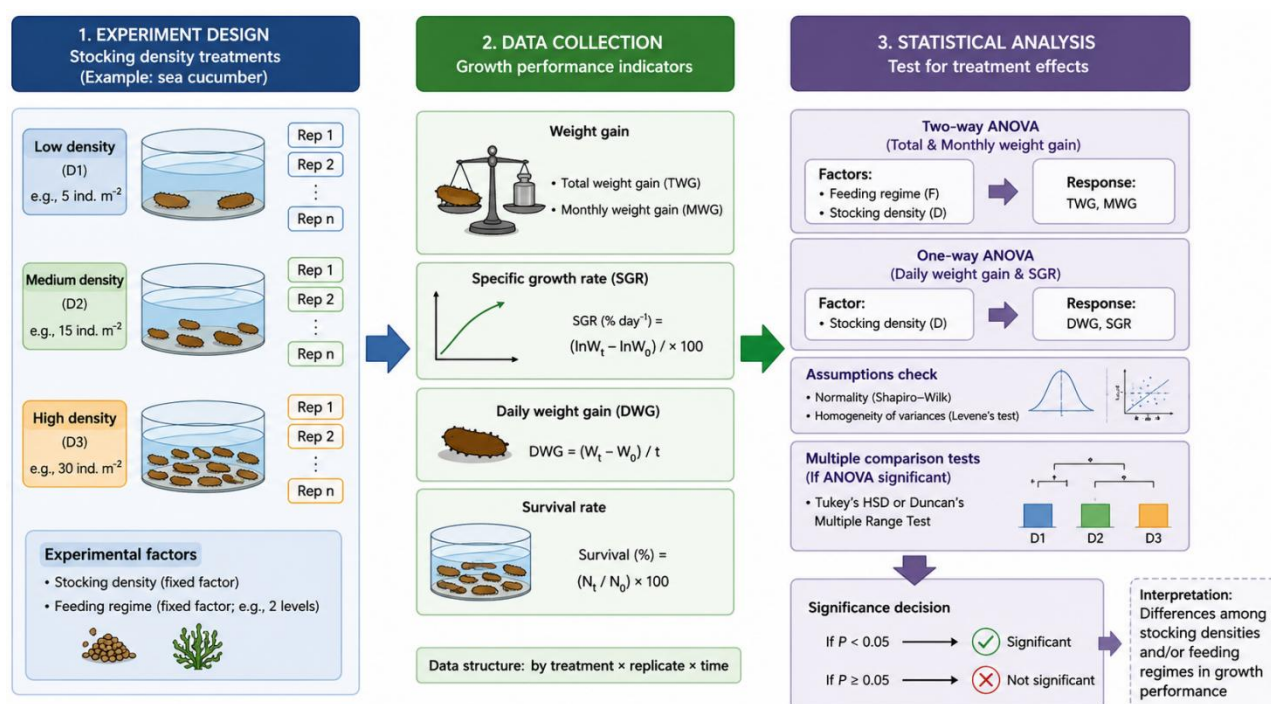


Figure 1 Statistical framework for analyzing stocking density effects on growth performance using ANOVA and multiple comparison tests in aquatic culture systems. Adapted from standard experimental designs in aquaculture growth studies

More advanced approaches combine regression modeling and resampling to capture continuous density-growth relationships. In a floating-cage study on spotted rose snapper, growth was modeled using von Bertalanffy, logistic and Gompertz curves, with model selection via Akaike and Bayesian information criteria, and the logistic model chosen as best (Jurado-Molina et al., 2023). Bootstrap simulations (1,000 runs per density) were then used to estimate the distribution of the instantaneous growth rate parameter (K) for each density, and ANOVA followed by Tukey HSD compared K among densities, revealing an optimal intermediate density not evident from simple length-at-age comparisons (Jurado-Molina et al., 2023).

5 Mechanisms Underlying the Effects of Stocking Density on Sea Cucumber Growth

5.1 Physiological mechanisms underlying the growth-promoting or growth-inhibiting effects of stocking density

Physiological responses to density determine whether stocking promotes or suppresses sea cucumber growth by shaping energy allocation between maintenance and somatic gain. Experiments on *Apostichopus japonicus* show that high densities elevate cortisol and lactate in coelomic fluid, while glucose declines, indicating chronic crowding stress that accelerates energy consumption and reduces resources available for tissue growth. In contrast, moderate densities can enhance metabolic activity and nutrient utilization, as shown by higher metabolizable energy, excretion energy and activities of key respiratory enzymes at intermediate stocking levels, which coincide with superior growth performance (Mei et al., 2022). Behavioral and neuroendocrine adjustments further mediate physiological effects of density on growth. Under high density, *A. japonicus* shows increased crawling in the short term but pronounced long-term inhibition of feeding, directly limiting energy intake and growth potential. Density also alters neurotransmitter profiles: γ -aminobutyric acid (GABA) increases significantly at high density, and transcriptomic changes in lipid and energy metabolism pathways have been observed, suggesting central regulation of behavior and metabolic partitioning that reinforces growth inhibition under crowding (Tian et al., 2024).

5.2 Ecological mechanisms regarding competition for substrate resources and space utilization efficiency

Ecologically, stocking density modifies competition for benthic food and sediment surface, thereby affecting growth and size structure within populations. In integrated mariculture of *Holothuria scabra* with *Eucheuma denticulatum*, low-density treatments showed the highest individual growth rates, whereas high-density treatments had the lowest,

attributed to intensified competition for food and space on or within the sediment. Similar patterns appear in *Holothuria tubulosa*, where juveniles stocked at 6 ind/m² achieved substantial weight gain, while those at 30 ind/m² exhibited negative growth and spent more time on tank walls, behavior interpreted as escape from crowded, resource-limited sediments. Space utilization efficiency also depends on how individuals partition habitat and cope with physical stressors. On NE Atlantic rocky reefs, *Holothuria arguinensis* densities and size distributions are shaped mainly by the ability to withstand hydrodynamic forces, enabling different size classes to use distinct microhabitats and thereby reduce direct competition for space and resources (Silva et al., 2023). In sea ranching of *Holothuria atra*, low-density cages achieved higher individual weight gain than high-density cages, and overcrowding led to fission and reduced body size, reflecting ecological limits where critical biomass thresholds are determined by available sedimentary organic matter and microphytobenthos production (Hartati et al., 2020; Hartati and Zainuri, 2021).

5.3 Interactions between environmental factors and growth responses under different densities

Environmental factors such as temperature, disease pressure and organic loading interact with density to shape growth outcomes and survival. In *A. japonicus*, high-density groups exposed to bacterial challenge or acute temperature decrease showed elevated morbidity, suppressed righting and feeding behaviors, and increased superoxide dismutase and pyruvate kinase activities, indicating that crowding reduces stress resistance and amplifies the negative effects of additional environmental stresses (Tian et al., 2025). Larval stages show similar density-environment interactions: auricularia of *Parastichopus californicus* had reduced specific growth rates and metamorphosis at 8 inds/mL compared to ≤ 0.5 inds/mL, and optimal performance occurred only when density and microalgal ration were matched to favorable temperatures (16 °C -18 °C). Water and sediment quality conditions, themselves products of culture intensity, further mediate density effects. In an abalone-*Neostichopus grammatus* IMTA system, higher sea cucumber density significantly lowered nitrite concentrations and, together with tank-cleaning frequency, shaped sludge organic matter and nutrient content, thereby influencing abalone growth even though sea cucumber growth remained unaffected (Onomu et al., 2024). In ponds for *A. japonicus* seedlings, temporal changes in phytoplankton biomass, particulate organic matter and chlorophyll-a provide both food and environmental cues; such dynamics imply that a density suitable at one time may exceed carrying capacity when plankton and particulate food decline later in the season (Wu et al., 2026).

6 Growth Responses of Sea Cucumber Under Different Stocking Densities

6.1 Comparison of growth differences under various stocking densities

Growth comparisons across densities consistently show that individual performance declines as crowding increases, although the optimum level varies by species and system. In juvenile *Holothuria tubulosa*, mean weight gain was about 29.5 g at 6 ind/m² but fell to 3.0 g at 15 ind/m² and became negative (-4.4 g) at 30 ind/m², with specific growth rate decreasing significantly as density increased. Similar patterns were observed in *Holothuria scabra* integrated with seaweed, where sea cucumbers at low density (150 g/m²) had the highest mean growth rate (0.80 g/d), while growth dropped markedly at high density. For *Apostichopus japonicus*, both tank and field studies indicate that specific growth rate and body weight decline with increasing biomass, and that intermediate densities may be optimal. In a full-sib fast-growing strain, body weight and SGR decreased significantly as density increased from 130 to 220 days, and regression modeling identified an optimal initial density of 24.4 g/m² for seedling production. Field grow-out with three size classes showed that small individuals had higher growth rates (0.63%/d) than medium and large across densities, implying that growth responses to density are size-dependent and that density settings should be adjusted as animals grow.

6.2 Analysis of density effects on survival rate and health status

Survival generally remains high at low to moderate densities but declines when biomass exceeds system carrying capacity or when high density interacts with other stressors. For *A. japonicus* in indoor tanks, survival stayed between 90%-100% at 1-5 ind per 10 L but dropped to 72% at 10 ind per 10 L, indicating a threshold beyond which crowding compromises survival. In net-cage culture, survival at the highest biomass (850 g/m²) was 73%, lower than 78%-89% at 150-600 g/m², again showing density-dependent mortality. High density also acts as a chronic

stressor that affects endocrine status, energy allocation and disease resistance. In *A. japonicus*, increasing density altered cortisol, lactate and glucose profiles, with small individuals showing significantly higher cortisol at high densities and greater changes in lactate and glucose, indicating elevated stress and energy consumption that ultimately reduced growth and biochemical reserves. Under bacterial challenge and acute temperature decrease, high density increased morbidity and inhibited righting and feeding behaviors, while antioxidant (SOD) and metabolic (PK) enzymes were elevated, helping explain decreased stress resistance and higher mortality risk at crowded conditions (Tian et al., 2025).

6.3 Evaluation of correlations between environmental factors and growth performance

Environmental conditions interact with density to shape growth responses, particularly via organic loading and water quality. In open-water IMTA, *Holothuria poli* stocked under fish cages at sites 10-25 m from the pens had positive SGR (0.18%-0.20%/d), whereas animals at a reference site showed no average growth; however, mass mortalities occurred directly beneath cages due to smothering by settled wastes, despite dissolved oxygen levels above lethal thresholds (Cutajar et al., 2022). In *H. scabra*-seaweed co-culture, sediment TOM and TOC decreased at medium sea cucumber density but accumulated at low and high densities, and growth rates were highest at low density, indicating that both benthic food supply and self-induced organic enrichment mediate density-growth relationships. Temperature is another key covariate, with both optimal windows and thresholds interacting with density. For California sea cucumbers, auricularia larvae showed highest SGR and metamorphosis at 16-18 °C, and survival peaked at 16 °C, suggesting that sub- or supra-optimal temperatures could narrow the density range that supports good growth and metamorphosis. For a fast-growing *A. japonicus* strain, rapid growth and pronounced density-related variation occurred at an average of 19.7 ± 1.3 °C, illustrating that near-optimal temperatures can amplify both growth and inter-individual differences as density rises.

7 Case Study: Evaluation of Sea Cucumber Growth Under Practical Stocking Density Management

7.1 Analysis of practical applications of different density management models at a typical farm

On tropical farms culturing *Holothuria scabra*, producers commonly combine earthen nursery ponds, community sea pens and sea ranching areas, adjusting stocking densities across units to balance growth, survival and operational costs. Earthen ponds are reported as the most effective units for nursery rearing juveniles to stocking size, with growth and survival to market size considered favorable, but further improvements are expected through experiments on stocking density, feeding regimes and pond management. Sea pens and sea ranching are used as grow-out and stock-enhancement models, but they differ in security and density control: pens confer ownership yet incur costs for materials and surveillance, whereas ranching spreads animals over large leased areas at low per-area density, trading density control for lower infrastructure investment. At integrated multi-trophic aquaculture (IMTA) sites, density management must simultaneously support growth and bioremediation. A Mediterranean fish farm co-culturing *Holothuria poli* below cages showed that sea cucumber survival and growth depended on cage positioning and organic load, with mass mortalities directly under the cage due to smothering by settled wastes, and better specific growth rates at moderate distances from the farm (Cutajar et al., 2022). Practical density management on such farms therefore relies on matching stocking levels and cage placement to modeled waste footprints, ensuring that sea cucumbers receive sufficient organic inputs without exceeding local benthic carrying capacity (Figure 2) (Sadoul et al., 2022; Grosso et al., 2023).

7.2 Production issues and optimization measures under high-density culture conditions

High-density culture is attractive for maximizing output per unit area but frequently introduces production problems related to crowding stress, disease, and water and sediment quality. In *Apostichopus japonicus*, high stocking density increased morbidity and suppressed feeding under bacterial challenge and acute temperature decreases, while antioxidant (SOD) and metabolic (PK) enzyme activities rose, indicating reduced stress resistance and higher maintenance costs that can depress growth (Tian et al., 2025). Similarly, behavioral and transcriptomic analyses show that chronic high density inhibits long-term feeding, alters neurotransmitter levels and affects lipid and energy metabolism pathways, helping to explain why growth often stagnates or declines when densities exceed critical

thresholds (Tian et al., 2024). On farms, optimization measures combine density control with husbandry adaptations. In intensive *H. scabra* culture, providing highly nutritious diets and appropriate feeding regimes can partially compensate for food competition at higher densities, improving feed conversion and protein efficiency, though excess crowding still reduces growth. In land-based IMTA tanks, adjusting sea cucumber density and tank-cleaning frequency can optimize bioremediation and co-cultured species performance: higher *Neostichopus grammatus* density lowered nitrite and, at an intermediate cleaning frequency, improved abalone mean weight without affecting sea cucumber growth, illustrating that careful density-management combinations can alleviate some high-density issues (Onomu et al., 2024).

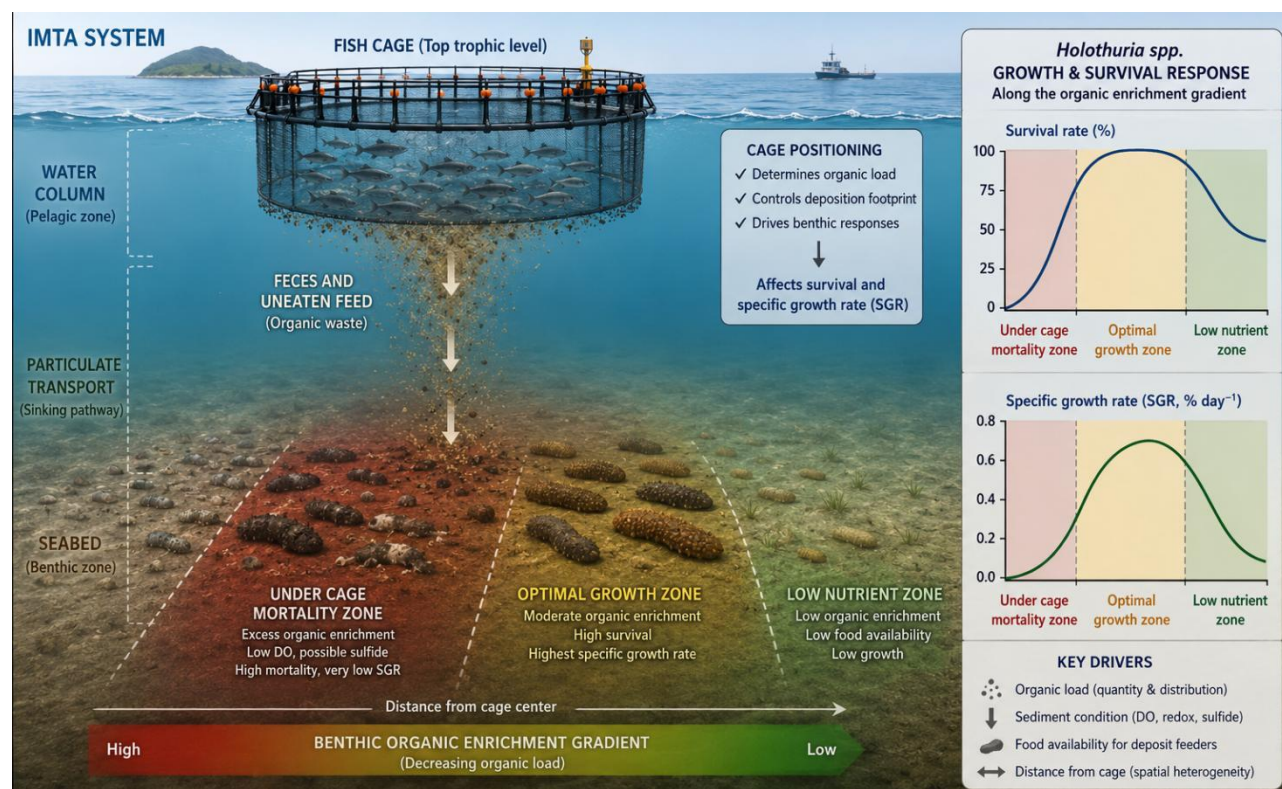


Figure 2 Schematic representation of integrated multi-trophic aquaculture (IMTA) systems showing organic matter deposition gradients and spatial variation in *Holothuria* spp. growth and survival

7.3 Comprehensive assessment of economic and ecological benefits based on field data

Field studies at community sea-pen farms and ranching sites demonstrate that stocking density management directly influences both economic returns and ecological co-benefits. In tropical *H. scabra* mariculture, cost-benefit analyses show that labour and utility costs can preclude profitability of monoculture pond farming, pushing farmers toward co-culture or lower-cost sea ranching, with profitability shaped by growth to larger body sizes that fetch exponentially higher prices (Azari et al., 2021). At a village-scale farm in Madagascar, pens stocked with *H. scabra* at relatively high densities (~300 g/m²) significantly increased leaf extension rates of the dominant seagrass *Thalassia hemprichii* by about 30%, indicating that income-generating sea cucumber farming can simultaneously enhance key coastal habitats (Arnall et al., 2021). At the fish-farm scale, modeling and IMTA assessments reveal trade-offs between stocking density, bioremediation performance and broader environmental impacts. An integrated red drum-*H. scabra* system showed that co-culture reduced eutrophication impacts and net primary production use relative to finfish monoculture, but only slightly lowered net particulate waste because current limits to sea cucumber stocking density constrain bioremediation potential (Chary et al., 2020). More generally, reviews emphasize that exceeding optimal stocking densities may improve local organic matter bioremediation but compromise sea cucumber growth yield, and call for more comprehensive economic evaluations of large-scale IMTA systems including high-value holothurians (Ciriminna et al., 2024).

8 Conclusion

Across species and culture systems, the evidence shows that stocking density exerts a primary control on growth performance, feed utilization and energy allocation in sea cucumbers. Growth rates, specific growth rate and relative weight gain consistently decline as density increases, with high-density groups often exhibiting negligible or even negative weight change, as demonstrated for juvenile *Holothuria tubulosa* and several other Mediterranean species. High densities also modify energy budgets and endocrine status: in *Apostichopus japonicus*, increasing density reduces apparent digestibility, food conversion efficiency and energy for growth, while elevating cortisol and lactate, indicating chronic crowding stress. Stocking density further affects within-cohort variability and health status. For *A. japonicus*, the coefficient of variation in body weight and differentiation in cortisol responses between large and small individuals increase with density, implying that crowding accentuates growth inequality and may predispose smaller animals to poorer performance. Under additional stressors such as bacterial challenge or acute temperature decrease, high density increases morbidity and suppresses righting and feeding behaviors, confirming that crowding not only reduces growth but also compromises stress resistance and overall health.

Despite species- and system-specific differences, a coherent pattern emerges in which low to moderate densities optimize individual growth and survival, whereas higher densities are suitable only for short-term handling. For juvenile *H. tubulosa* (~40 g) in tanks, 6 ind/m² (~250 g/m²) yielded substantial weight gain and positive SGR, while 15 ind/m² produced negligible growth and 30 ind/m² led to negative biomass change, leading to a recommendation of 6 ind/m² for grow-out and explicit avoidance of 30 ind/m². For *H. arguinensis* and *H. mammata*, optimal tank-based densities were identified as 1 ind per 0.2 m² and 5 ind per 0.5 m² respectively, with critical biomass thresholds (~472 and 988 g/m²) above which growth ceased, suggesting that both numerical density and biomass should guide management. In pond and net-enclosure systems, optimal densities for *A. japonicus* depend on feeding regimes and management goals. Long-term pond trials fitted with B–N curves identified optimal stocking densities of 22.3 ind/m² under feed-supplement and 14.1 ind/m² without feed for maximizing net production, reflecting trade-offs between individual growth and total yield. At the industry level, reviews of Mediterranean and NE Atlantic species highlight that medium densities (600–700 g/m²) can be tolerated briefly for operations such as transfer and cleaning, but high densities and biomass above species-specific critical values should be avoided in routine production to prevent negative growth and health problems.

Current research on stocking density remains constrained by species and regional focus, methodological inconsistency and limited integration with economic and environmental objectives. Systematic review of NE Atlantic and Mediterranean species reveals that most work has concentrated on a few taxa such as *H. tubulosa*, *H. arguinensis* and *H. mammata*, with sparse data for others, and that critical biomass values and recommended densities vary widely, necessitating species-specific tests and standardized protocols. At the same time, large-scale industry reviews from China and the tropics emphasize that despite rapid expansion of sea cucumber farming, many stocking density decisions are still empirical, and there is a lack of well-designed, long-term experiments and meta-analyses to guide best practice across culture models. Future research should couple density manipulation with mechanistic studies on physiology, genetics and behavior, and with multi-objective optimization that includes growth, health, product quality and ecosystem services. Physiological and endocrine work has already shown that density acts as an environmental stressor that alters cortisol dynamics, energy budgets and gene expression, but these insights are rarely incorporated into farm-level management models. Strategic papers on industry development in China call for advances in basic biology, behavioral studies, selective breeding and ecological culture technologies, which together could enable density recommendations that are tailored to strains, environments and integrated multi-trophic systems, supporting both sustainable production and environmental protection.

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Feature Review

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Characteristics of Disease Occurrence in Oyster Farming

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Abstract Oyster aquaculture is an important component of global marine fisheries, yet disease outbreaks have become a major constraint on its sustainable development. This paper systematically analyzes the characteristics of disease occurrence in oyster farming by integrating biological susceptibility, pathogen diversity, environmental drivers, transmission pathways, host immune responses, and epidemiological patterns. The results indicate that oysters are highly vulnerable to pathogenic infections due to their filter-feeding behavior and limited adaptive immune capacity. Bacterial diseases, particularly those caused by *Vibrio* species, are the most frequently reported, followed by viral, parasitic, and fungal infections. Environmental stressors such as elevated water temperature, salinity fluctuation, dissolved oxygen depletion, and eutrophication significantly increase disease incidence by weakening host immunity and promoting pathogen proliferation. High stocking density further accelerates disease transmission through waterborne pathways and aquaculture facility-mediated spread. In addition, microbial community dysbiosis plays a critical role in disease development and progression. A case study of intensive farming systems demonstrates that poor environmental management and inadequate biosecurity measures can lead to rapid disease outbreaks and substantial economic losses. Based on these findings, integrated disease management strategies combining ecological regulation, pathogen monitoring, and improved farming practices are proposed to enhance disease prevention and control in oyster aquaculture.

Keywords Oyster aquaculture; Disease occurrence; Pathogen dynamics; Environmental stress; Disease management

1 Introduction

Oyster aquaculture has become one of the most important components of global seafood production, expanding rapidly as demand for sustainable animal protein grows. Oysters are now among the most widely farmed molluscs, with several commercial species cultivated worldwide, and global output has climbed into the multi-million-tonne range as producers respond to rising consumer interest in nutritious seafood (Okon et al., 2023). Within this expanding sector, the Pacific oyster *Crassostrea gigas* dominates production and underpins the economies of many coastal regions; yet the industry remains highly vulnerable to disease, environmental change and management constraints that limit producers' ability to fully exploit growing markets (Botta et al., 2020; Petton et al., 2021). Over the past decade, infectious diseases have emerged as a central constraint on oyster farming, with repeated mass mortality events reported from major producing regions. In Pacific oysters, outbreaks associated with Ostreid herpesvirus 1 and *Vibrio* bacteria have intensified since 2008, increasing in both severity and geographic extent and making disease a particularly sensitive issue for producers (Alfaro et al., 2019). Pacific oyster mortality syndrome (POMS), driven by OsHV-1 μ Var and subsequent bacterial dysbiosis, has become panzootic and now affects juvenile oysters in multiple countries, illustrating how complex host-pathogen-environment interactions can produce recurrent, large-scale losses (Petton et al., 2021). The economic and social consequences of these disease events are profound, with massive mortalities sometimes causing near-total stock losses and threatening the viability of farms and coastal communities. For POMS alone, annual juvenile mortality in France has been estimated to exceed 35% of cultivated and natural oysters, illustrating the scale at which disease can erode production and income. At the broader aquaculture scale, diseases across species are estimated to cost billions of dollars annually, yet economic assessments remain sparse, underscoring the need for more systematic evaluations of losses and of the benefits of control strategies in oyster systems (Maezono et al., 2025). Against this backdrop, there is a pressing need to better characterize the patterns and drivers of disease occurrence in real farming contexts so that risk can be

managed more effectively. Current knowledge shows that oyster disease expression is influenced by a suite of interacting host, pathogen and environmental factors-such as oyster age and genetics, temperature, food availability and microbiota-but the mechanisms by which these variables jointly control outbreaks remain poorly resolved. The present study therefore focuses on describing the characteristics of disease occurrence in oyster farming-across space, time, production stages and environmental gradients-with the dual objectives of identifying key risk factors and providing an empirical basis for improved surveillance and management strategies (Petton et al., 2021).

2 Biological and Ecological Basis of Oyster Disease Susceptibility

2.1 Oyster physiological characteristics and immune defense systems

Oysters rely entirely on a sophisticated innate immune system to survive in pathogen-rich estuarine environments, compensating for the absence of adaptive immunity. Hemocytes circulating in the hemolymph execute core defenses including immune recognition, signal transduction, synthesis of antimicrobial peptides, phagocytosis and encapsulation, supported by apoptosis and autophagy as important immune mechanisms (Wang et al., 2018). Single-cell transcriptomic analyses have revealed at least seven functionally distinct hemocyte types and multiple hematopoietic lineages, with specialized roles such as phagocytosis, reactive oxygen species production, copper accumulation and antimicrobial peptide expression, underscoring the cellular complexity behind disease resistance (De La Forest Divonne et al., 2025). Oyster immunity also shows plasticity and memory-like features that shape disease outcomes in farming. Immune priming and maternal immune transfer have been reported, suggesting that prior exposure can modulate subsequent responses, and neuroendocrine systems (catecholaminergic, cholinergic, neuropeptide and GABAergic) further regulate these defenses (Wang et al., 2018). Experimental work shows that inactivated Ostreid herpesvirus-1 and related viral antigens can rapidly stimulate hemocyte functions (e.g. ROS production, immune-related gene expression) without cytotoxicity, highlighting the potential to exploit innate “immune memory” and hemocyte responsiveness to reduce mortality from Pacific oyster mortality syndrome (Delisle et al., 2023).

2.2 Filter-feeding ecological habits and environmental exposure characteristics

As sessile filter feeders, oysters continuously pump large volumes of water, concentrating microorganisms and particles from their environment. An individual can retain up to 75% of microorganisms present in surrounding water, so naturally occurring bacterial communities, including potentially pathogenic taxa, accumulate in tissues and can pose health risks, particularly when animals originate from poor-quality environments (Mendes et al., 2023). Long-term monitoring at a commercial Pacific oyster area showed that, while oysters exhibited good depurating capacity for fecal bacteria (*E. coli*, enterococci) compared with surrounding waters, norovirus persisted seasonally in digestive glands, illustrating that filter feeding exposes oysters to diverse microbes and that clearance efficiency is pathogen-dependent (Rodrigues et al., 2023). Filter feeding also structures host-microbiota-pathogen interactions that influence disease susceptibility and food safety. Comparative analyses of water and oyster microbiota found that environmental conditions strongly shaped water communities and pathogen levels, whereas oyster digestive gland communities were more stable and showed “hot oyster” patterns, where individual oysters accumulated much higher *Vibrio* or fecal indicator loads than neighbors (Diner et al., 2023). In estuarine culture sites, surveys of *Crassostrea gasar* and surrounding waters have repeatedly detected human-pathogenic bacteria such as *Escherichia coli*, *Salmonella*, *Vibrio* spp. and others in both oysters and environment, confirming that filter-feeding oysters mirror-and can amplify-microbial risks associated with degraded water quality (Mendes et al., 2023).

2.3 Mechanisms linking environmental stress to disease susceptibility

Environmental stressors modulate both pathogens and host defenses, creating windows of high disease susceptibility in oyster farming. Large-scale field and modeling studies demonstrate that seawater temperature is a dominant driver of disease-induced mortality in Pacific oysters, with mortality risk sharply increasing between about 16 °C-24 °C and specific mean temperature thresholds (around 19 °C-24 °C over 12-21 days) corresponding to high probabilities of OsHV-1 outbreaks and substantial stock losses (Shi et al., 2024). A four-year, multi-site survival analysis similarly identified seawater temperature as the strongest predictor of mortality, with additional modulation by wind speed and humidity, and showed that spat were far more vulnerable than juveniles or adults, indicating that

environmental forcing interacts with life stage to shape disease patterns (Fleury et al., 2025). Other stressors, including salinity fluctuations, low flow and hypoxia, affect host-pathogen interactions and immune competence. Experimental manipulation of flow, temperature, salinity and dissolved oxygen showed that oysters in low-flow, high-sedimentation microhabitats had the greatest *Perkinsus marinus* infection prevalence, intensity and mortality, with disease responses significantly negatively correlated with flow, likely due to poorer physiological condition under chronic stress. At the cellular level, hypoxia experiments revealed that granulocytes under moderate low oxygen could transiently enhance phagocytosis and deploy antioxidant and mitophagy responses, but severe hypoxia led to ROS accumulation, mitochondrial dysfunction and impaired lysosomal degradation, suggesting that prolonged or intense hypoxia can overwhelm hemocyte resilience and thereby heighten disease susceptibility (Chen and Wang, 2025).

3 Major Pathogens and Disease Spectrum in Oyster Aquaculture

3.1 Bacterial diseases and the pathogenicity of *Vibrio* species

Bacterial diseases in oyster aquaculture are dominated by *Vibrio* spp., which occur as part of the normal microbiota but include lineages that cause severe mortality. Many *Vibrio* species from the *Splendidus* and *Harveyi* clades are frequently associated with bivalves, and several have been linked to mortality outbreaks as primary or opportunistic pathogens in cultured oysters (Destoumieux-Garzón et al., 2020). Even in non-intensive farming areas without recorded mass mortalities, Pacific oysters can naturally harbor potentially pathogenic *Vibrio* strains, indicating that virulence is present in the microbial community before overt disease is observed (Oyanedel et al., 2022). Specific pathogenic *Vibrio* species and lineages have been identified in large-scale mortality events. In China, mass summer mortality of *Crassostrea gigas* with over 60% losses was associated with *Vibrio alginolyticus*, whose virulence was confirmed experimentally and enhanced at higher temperatures, highlighting temperature-dependent pathogenicity (Wang et al., 2021; Yang et al., 2021). In Europe, *Vibrio aestuarianus* subsp. *francensis* emerged as a specialist oyster pathogen causing recurrent adult mortalities with ~25% mortality rates and shows genomic adaptations such as a copper-resistance island that may favor persistence in oyster hosts (Mesnil et al., 2023).

3.2 Viral diseases and their epidemiological characteristics

Viral infections, especially those caused by Ostreid herpesvirus 1 (OsHV-1) and its microvariants, are a major cause of disease in oyster aquaculture. OsHV-1 has been detected in at least 15 countries and is associated with massive mortalities in *Crassostrea gigas*, with microvariants such as OsHV-1 μ Var driving Pacific oyster mortality syndrome (POMS) that has become panzootic (Alfaro et al., 2019). Descriptive epidemiology from the Hawkesbury River estuary in Australia showed that OsHV-1-associated mass mortalities affected all age classes but were most severe in spat and juveniles, with incubation periods of less than 4 days and evidence of subclinical infection months before overt mortality. Epidemiological studies highlight strong influences of temperature, host age and viral genotype on disease expression. Long-term sentinel monitoring in Australian estuaries found that OsHV-1 mortality typically began when mean water temperature exceeded ~20 °C, with consistent seasonal windows of high risk and spatial clustering at the scale of farms and even baskets. Experimental infections comparing OsHV-1 microvariants isolated between 2011 and 2015 in Australia showed significant reductions in virulence over time, with earlier isolates causing higher hazard of death and cumulative mortality, suggesting that phenotypic variation among genotypes may alter outbreak severity and offering prospects for management using low-virulence strains (Cain et al., 2021).

3.3 Types and impacts of parasitic and fungal diseases

Protozoan parasites of the genera *Perkinsus* and *Haplosporidium* constitute some of the most significant non-viral, non-bacterial threats in oyster aquaculture. In eastern oysters along the U.S. Atlantic and Gulf coasts, *Perkinsus marinus* (dermo) and *Haplosporidium nelsoni* (MSX) are prevalent and have been identified as causative agents of fatal diseases that have triggered mass mortalities and constrained population recovery. (Batchelor et al., 2023). Recent qPCR-based surveys in Georgia and Maine show very high prevalence of *P. marinus* and *H. nelsoni* (often >80 %–90%), with complex relationships to oyster condition that may include emerging resistance or tolerance in some populations despite historical die-offs (Marquis et al., 2020; Batchelor et al., 2023). Other parasitic diseases, notably bonamiasis, have caused severe localized impacts in flat oyster industries and may co-occur with

Perkinsus infections. In Australia, bonamiasis in *Ostrea angasi* led to mass mortalities in a pilot native oyster industry in the 1990s, and a subsequent epizootic in 2015 was attributed to *Bonamia exitiosa*, with *Perkinsus olseni* also reported for the first time in this host, underscoring the potential for multiple protozoan agents to affect emerging aquaculture species (Bradley et al., 2025). Historical syntheses further identify *Roseovarius* oyster disease and disseminated neoplasia as additional important disease conditions in some regions, emphasizing that the pathogen spectrum in oyster aquaculture extends beyond vibrios and OsHV-1 to a diverse assemblage of protozoan and other agents whose distributions may shift with climate and industry expansion.

4 Environmental Drivers of Disease Occurrence in Oyster Farming

4.1 Effects of fluctuations in water temperature, salinity, and dissolved oxygen

Water temperature is a key driver of major oyster diseases, directly affecting both host susceptibility and pathogen replication. Controlled challenges with OsHV-1 μ Var showed mortality of Pacific oysters reaching 77 °C-84% at 22 °C-26 °C, but dropping to 23% at 18 °C and 0% at 14 °C, with a clear threshold between 14 °C-18 °C below which productive infection did not occur. Broader analyses indicate that climate-driven warming alters pathogen growth rates, spatial dispersion and host physiology, thereby increasing the severity and frequency of oyster disease outbreaks at global scale (Okon et al., 2023). Salinity and dissolved oxygen interact with temperature to modify disease risk. Experimental work on OsHV-1 showed that oysters acclimated to low salinity (10‰) had very high survival (>95%) after exposure, whereas those at 15-35‰ survived at only 43 °C-73%; however, non-acclimated oysters suffered 23% survival at 10‰, suggesting mortality from salinity shock rather than viral disease. In estuaries with diel-cycling hypoxia, oysters exposed to repeated low dissolved oxygen experienced increased acquisition and progression of *Perkinsus marinus* infections and reduced growth, implicating hypoxia-induced immune impairment as a mechanism enhancing disease susceptibility.

4.2 Role of eutrophication and water pollution in promoting disease

Nutrient enrichment and pollution reshape microbial communities in coastal habitats and can elevate pathogen loads relevant to oyster health. Along a eutrophication gradient in an urbanized estuary, oyster gut microbiomes showed functional shifts in nutrient-cycling genes that tracked local nutrient regimes, indicating that eutrophication alters oyster-associated microbial functions potentially linked to host physiology and disease risk (Figure 1) (Stevick et al., 2021). In seagrass sediments near nutrient sources, putative pathogen groups such as *Vibrio* spp. and *Pseudoalteromonas* spp. doubled in relative abundance compared with less enriched sites, suggesting that nutrient pollution can increase environmental reservoirs of bacterial pathogens affecting invertebrates and humans. More generally, climate-driven change and pollution jointly promote pathogen development and disease exposure in oysters. A global review highlights that climate change fosters proliferation of aquatic pathogens and harmful algal blooms, while pollution and other environmental burdens compound these pressures, disrupting oyster biochemical pathways and physiological functions and leading to more frequent outbreaks (Okon et al., 2023). Conceptual work on oyster disease further emphasizes that shifting environmental parameters-including nutrients and pollutants-can alter both oyster immunity and pathogen growth and virulence, often via changes in the microbiome that buffer or amplify disease expression.

4.3 Mechanisms by which extreme weather and sudden environmental changes trigger disease

Extreme events such as marine heatwaves and intense rainfall can rapidly push environmental conditions beyond oyster tolerance thresholds and trigger disease-linked mass mortalities. A 24-week experiment during a summer mortality event recorded three mortality phases in Pacific oysters; the transition to a sharp mortality increase coincided with heavy rainfall, a 13-day marine heatwave up to 27.7 °C, reduced salinity (34.6 to 31.4 psu) and increased *Vibrio* abundance, with mortality positively correlated to the heatwave and *Vibrio*, and negatively to salinity (Siboni et al., 2024). Experimental simulation of a marine heatwave (20 °C -25 °C) led to 77.4% mortality in *C. gigas*, whereas mortality dropped to 4.3% when antibiotics were added; heat stress caused large increases in *Vibrio harveyi* and *V. fortis* within the microbiome, indicating that sudden warming can trigger dysbiosis and opportunistic bacterial disease. Extreme precipitation and freshwater inflow can likewise induce large-scale mortality through prolonged low salinity and associated stress-disease interactions. After Hurricane Harvey, mean

oyster mortality in Galveston Bay rose from 11% to 48%, reaching 100% at some reefs; mortality was significantly correlated with the duration of bottom salinity below 5 psu, while storm-induced sediment deposition showed no such relationship, implicating extended low-salinity exposure as the main driver (Du et al., 2021). A similar pattern was observed when a series of atmospheric rivers produced extreme freshwater discharge into San Francisco Bay, causing sustained salinities below ~6.3 and a near-100% mass mortality of wild oysters, closely matching critical salinity tolerances and highlighting how rare events can wipe out already depleted populations.

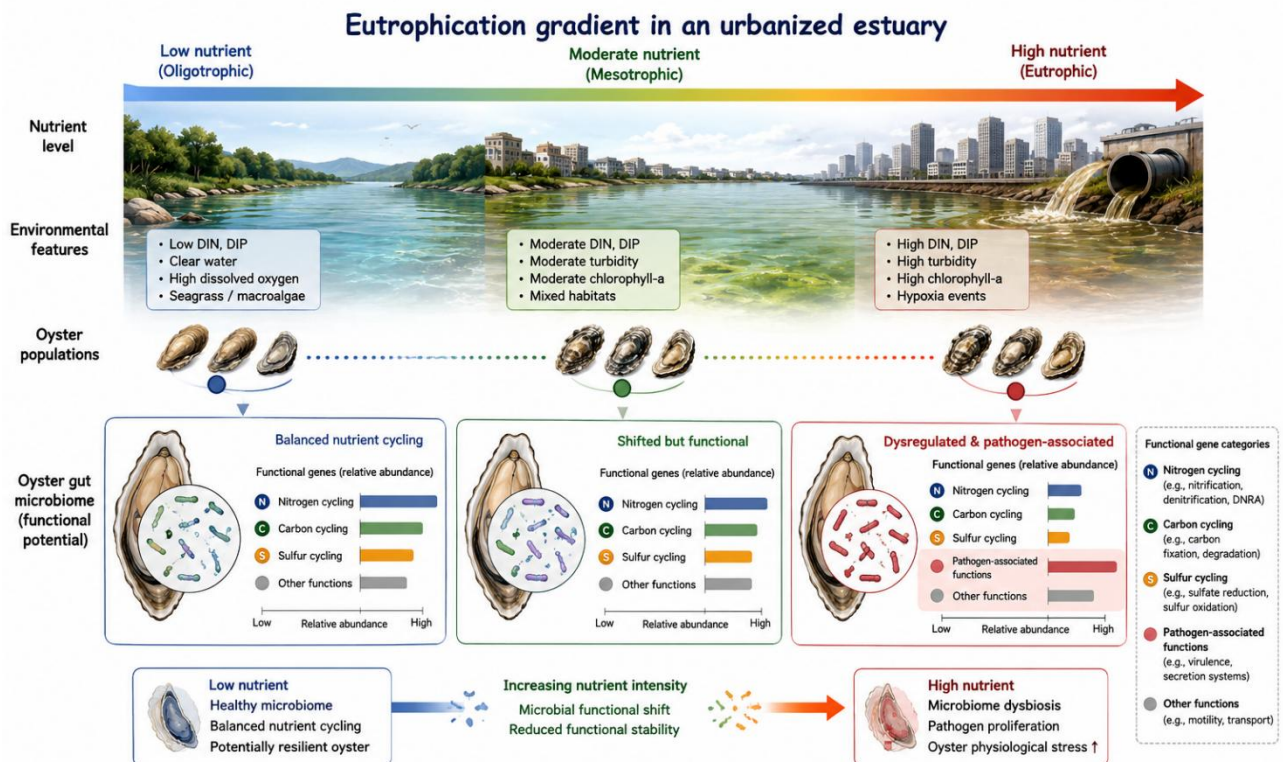


Figure 1 Changes in oyster gut microbiome functional profiles along an estuarine eutrophication gradient. Nutrient enrichment alters microbial functional genes associated with nutrient cycling, suggesting a link between eutrophication intensity, microbial dysbiosis, and potential host physiological stress

5 Disease Transmission and Epidemiological Characteristics

5.1 Waterborne transmission and density-dependent spread mechanisms

Experimental and modeling work for *Vibrio aestuarianus* shows clear waterborne transmission, with a basic reproduction number (R_0) around 2.9 and a generation time of ~5.5 days in small, closed oyster populations. (Lupo et al., 2020). Transmission is dose-dependent, driven by bacterial shedding and the concentration in seawater, implying threshold exposure levels needed to initiate an epidemic. At bay scale, hydrodynamic connectivity and temperature control the spatial spread of waterborne bacteria, allowing long-distance dispersal between distant farms over months. Theoretical models of marine infectious diseases further emphasize that highly infected oysters and the balance between pathogen release and removal in the water column determine outbreak thresholds and the existence (or not) of low-abundance refuges.

5.2 Transmission via aquaculture facilities and biological vectors

Recirculating and hatchery-like systems modify but do not eliminate waterborne viral circulation: OsHV-1 persists in seawater despite biofiltration and UV, and detection odds are higher where treatment is interrupted, showing facility design directly affects pathogen loads. Cohabitation experiments show higher donor biomass and feeding (algal addition) markedly increase OsHV-1 transmission and mortality, indicating facility management of stocking and feeding influences effective dose exposure. Field observations in Woollooware Bay show clustered OsHV-1 mortalities within farms and vertical stratification in the water column, consistent with infection from common

environmental sources shaped by local hydrodynamics and farm layout. Laboratory and epidemiological evidence support a role for particles and biofouling communities (e.g., plankton, fouled oysters on equipment) in transporting OsHV-1 and other pathogens, though successful transmission via fouling organisms appears rare and complex (Fuhrmann et al., 2021).

5.3 Risks associated with seedstock circulation and inter-regional transmission

Network analyses of French oyster farming show highly dynamic, heterogeneous transfer patterns among farm categories and growing sites, with seasonal peaks in movements and specific sites acting as high-risk hubs for becoming infected or transmitting disease (Coralie et al., 2016). Spatial epidemiology of OsHV-1 shows mortality starting in dense farming areas and spreading kilometres outward, consistent with animal movements and waterborne export from seedstock hotspots, while connectivity to farms is a strong mortality risk factor for both juveniles and adults (Gangnery et al., 2019). Historically, large-scale imports of Pacific oyster stock into Europe in response to disease crises created a positive feedback loop between introductions of non-native species (including pathogens) and further stocking, with continuing vector activity inferred over decades. More broadly, anthropogenic vector analysis identifies movements of live growing stock and culture substrates as among the highest-risk vectors in shellfish aquaculture networks, logistically difficult to manage but central to disease spread pathways across regions (Lovett et al., 2024).

6 Host Immune Response and Pathophysiological Mechanisms

6.1 Innate immune system and changes in disease-resistance responses

The oyster innate immune system relies on circulating haemocytes and a highly expanded repertoire of recognition and effector genes, enabling pathogen detection, phagocytosis, oxidative killing, antimicrobial peptide production and apoptosis (Wang et al., 2018). During bacterial or viral outbreaks, these defences can be subverted; for example, *Vibrio aestuarianus* deregulates hemocyte oxidative metabolism, impairing cellular functions and survival (De Lorgeril et al., 2018). Disease resistance varies strongly among families and life stages. Resistant oysters show higher basal expression of stress and antiviral pathway genes (TLR-NF κ B, JAK-STAT, STING-RLR), supporting more robust responses to Pacific oyster mortality syndrome (POMS). In contrast, susceptible juveniles in field outbreaks sense pathogens and activate receptors and signaling, but fail to induce key antimicrobial, apoptotic and redox-homeostasis genes, leading to microbial overgrowth and high mortality.

6.2 Characteristics of tissue damage and metabolic disorders

Complex pathogenesis is well illustrated in POMS, where OsHV-1 μ Var first infects haemocytes, inducing an immunocompromised state that permits secondary bacterial invasion and fatal bacteraemia (Destoumieux-Garzón et al., 2024). Histopathological observations in experimental infections show invasion of connective tissues by opportunistic bacteria during dysbiosis, consistent with systemic sepsis as a terminal lesion pattern. (Delisle et al., 2022; Destoumieux-Garzón et al., 2024) Metabolic reprogramming is another key feature of pathophysiology. During intense OsHV-1 replication, oysters show increased glycolysis and altered mitochondrial porin (VDAC) levels, resembling a “Warburg effect” that redirects energy metabolism. Other pathogens induce broad metabolic and cellular stress responses; *Vibrio coralliilyticus* infection in larvae reduces feeding, mobilizes energy reserves, remodels fatty acids, and activates antioxidant and heat-shock defences alongside immune pathways.

6.3 Mechanisms of gut and microbial community imbalance

Oysters host tissue-specific, dynamic microbiota that differ from surrounding seawater and are shaped by both environment and host genetics. In healthy states, this microbiota contributes to immune education and homeostasis; antimicrobial peptides help fine-tune microbial communities (Destoumieux-Garzón et al., 2024). Under stress or disturbance, rare phylotypes are lost, overall diversity declines, and the coupling between host genetics and microbiome composition breaks down, suggesting stress-driven community destabilization (Lokmer et al., 2016). Dysbiosis is now recognized as central to major syndromes such as POMS and environmentally driven mass mortalities. In POMS, OsHV-1-induced immune suppression leads to microbiota destabilization, replacement of commensals by virulent communities, and spill-over of opportunistic bacteria into tissues, amplifying disease

severity (King et al., 2018; Destoumieux-Garzón et al., 2024). Abiotic stressors such as low salinity or high temperature further disrupt digestive microbiota, increase pathogenic taxa (e.g. *Vibrio*), and are linked with inflammatory dysregulation and higher mortality during *Vibrio* infections (Li et al., 2022; Li et al., 2023). Oyster disease in farming systems emerges from the interplay of innate immune capacity, tissue-level damage, metabolic reprogramming and microbiome stability. Viral and bacterial pathogens exploit immune weaknesses and energy constraints, while environmental stressors destabilize microbial communities and inflammatory control, tipping oysters from resistance toward dysbiosis, systemic infection and mortality.

7 Case Study: Disease Outbreak Characteristics in Intensive Oyster Farming Systems

7.1 Analysis of typical disease outbreak processes in high-density farming areas

In intensive Pacific oyster farming areas, mass mortality episodes typically begin within farming zones and then spread rapidly across leases and into surrounding waters, highlighting the amplifying effect of high host density and farm clustering on infection pressure. Outbreaks often show strong spatial and temporal dependence, with disease fronts progressing from intensively used farming sectors toward less stocked or peripheral sites, consistent with local transmission driven by waterborne dispersal and farm connectivity (Figure 2) (Richard et al., 2021). Outbreak timing is tightly linked to seasonal windows when temperature favours pathogen replication, and juvenile cohorts in dense nursery structures are usually affected first, often experiencing very high losses within short periods. Husbandry operations such as handling and high stocking densities can further intensify outbreaks, with evidence that recent manipulation and dense basket systems increase mortality relative to lower-density rope culture or standard stocking levels (De Kantzow et al., 2017).

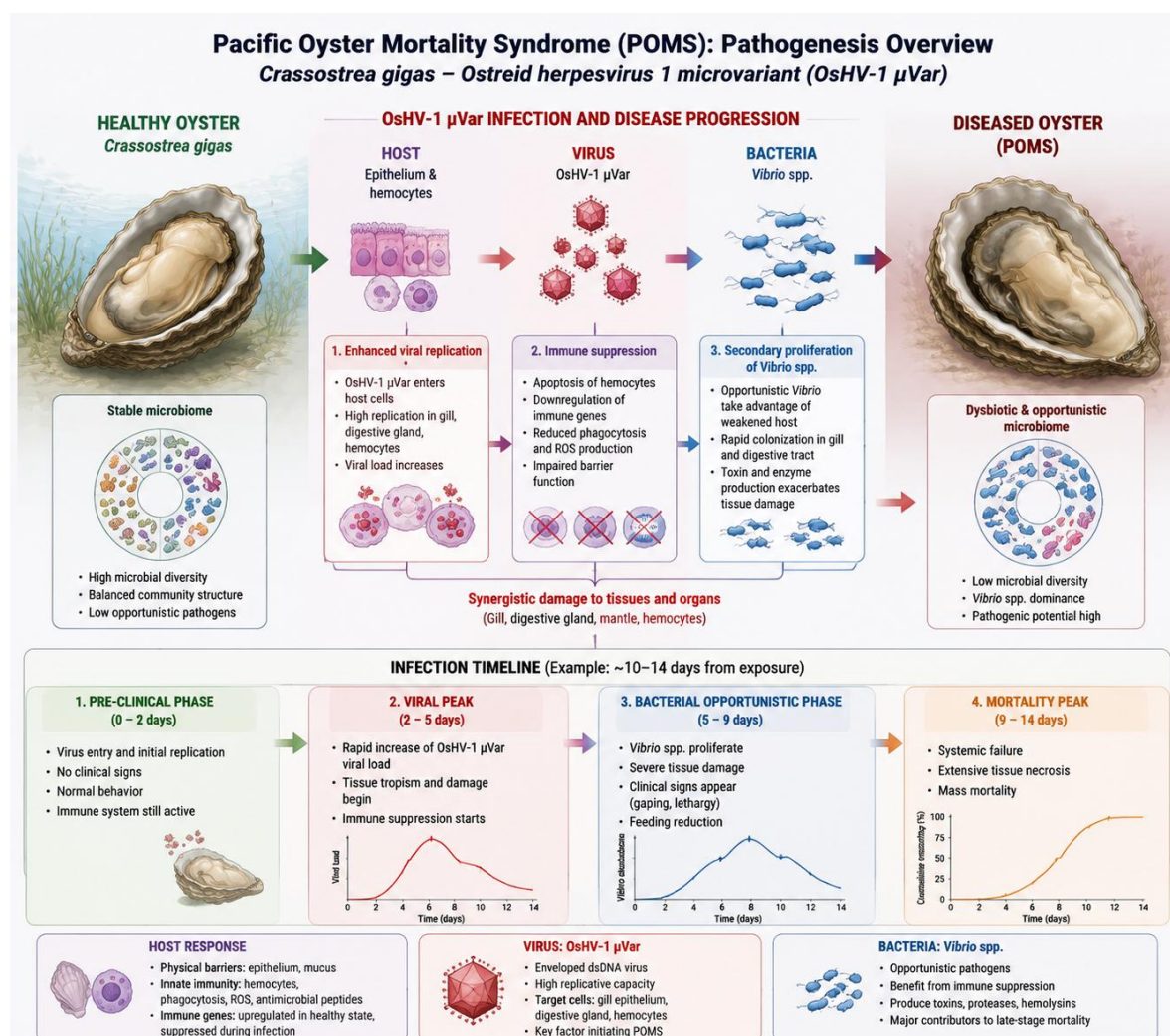


Figure 2 Pathogenesis cascade of Pacific Oyster Mortality Syndrome (POMS) in *Crassostrea gigas*

7.2 Identification of major pathogens and epidemiological dynamics

Across intensive systems, Pacific Oyster Mortality Syndrome (POMS) associated with Ostreid herpesvirus 1 microvariants (OsHV-1 μ Var) is the dominant cause of recurrent mass mortalities of *Crassostrea gigas* since 2008, often followed by opportunistic bacterial infections (Pernet et al., 2016). Epidemiological surveys also frequently implicate *Vibrio* spp., particularly *Vibrio aestuarianus* and other pathogenic vibrios, as co-factors or primary agents in some mortality events, with pathogen diversity contributing to variable clinical outcomes (Alfaro et al., 2019). Outbreak dynamics often follow a sequence in which OsHV-1 titres rise in oyster tissues before visible signs, peak around the mortality maximum, and are accompanied by shifts in bacterial communities towards known pathogenic genera (Richard et al., 2021). Environmental factors such as temperature thresholds and confinement influence both virus activation and bacterial proliferation, while host age, size, and genetic background modulate susceptibility, creating complex interaction patterns in intensive farms.

7.3 Evaluation of control measure effectiveness and economic losses

Because curative treatments and vaccination are not feasible, control in intensive oyster systems relies on risk-based husbandry, spatial planning and biosecurity, including movement restrictions and zoning, which can reduce infection pressure but have not prevented the global spread of OsHV-1 μ Var (Pernet et al., 2016). Adjustments in farming practices, such as optimizing stocking density, modifying culture structures or immersion regimes, and timing seeding to avoid high-risk temperature periods, have demonstrated reductions in mortality in some intensive settings. Economically, OsHV-1 microvariants have challenged the viability of Pacific oyster industries in both hemispheres, driving sector consolidation, loss of smaller farms, and shifts towards compensatory production strategies rather than purely technical disease solutions (Pernet et al., 2016; Fuhrmann et al., 2019). At a broader scale, marine diseases of farmed oysters and other aquaculture species impose economic burdens measured in billions of dollars annually, through direct losses, control costs, and regulatory compliance, underscoring the need for integrated, economically informed disease management in intensive oyster systems (Freitag et al., 2022).

8 Integrated Disease Management Strategies for Sustainable Oyster Farming

Ecologically informed farm placement and water-quality management can reduce disease risk. Spatial epidemiology of OsHV-1 shows that mortality is highest in inshore, high-biomass intertidal farming zones and decreases offshore, where better food quality and lower turbidity align with improved oyster health, indicating that maintaining good ecological status of coastal waters is a practical disease-mitigation strategy. Broader ecosystem-based perspectives argue that sustainable aquaculture must explicitly integrate organism health, environmental integrity, and human health, embedding disease control in wider ecosystem and food-system planning. Well-designed oyster culture can also act as a regulating service, filtering pathogens and reducing disease pressure on wild stocks when harvests occur before infected farmed oysters shed large quantities of parasites. At the farm scale, healthy-farming models emphasize carrying-capacity assessment, climate-change adaptation, and use of habitat features (e.g. mangroves, ecological floats) to buffer environmental stress and disease risk.

Selective breeding provides a powerful tool to reduce disease impacts where environmental control is limited. Reviews of breeding programmes show significant gains in resistance to major oyster pathogens (OsHV-1, *Haplosporidium nelsoni*, *Roseovarius crassostreae*, *Marteilia sydneyi*) after only a few generations, demonstrating that resistance is heritable and can be exploited to stabilize production. Family-based experiments in Pacific oysters confirm a strong genetic basis for resistance to OsHV-1 across life stages and show that improving OsHV-1 resistance does not compromise resistance to *Vibrio aestuarianus*, supporting multi-trait resistance breeding. Field mass-selection programmes have achieved dramatic survival improvements under OsHV-1 pressure, with selected lines of *Crassostrea gigas* reaching about 69% survival compared with 7% in controls after four generations, while also improving growth and yield. More recently, genomic selection has been shown to further accelerate gains in resistance to vibriosis, with genomic breeding values enabling discrimination between resistant and susceptible oysters and producing double-digit increases in survival and survival time in progeny, indicating a route to faster development of robust seedstock.

Effective integrated management requires surveillance systems designed for early detection rather than only proof of disease freedom. Expert-guided design for OsHV-1 highlights that observational (farmer-based) surveillance, when carefully structured and combined with targeted active sampling and strong industry-government partnerships, can greatly enhance system sensitivity and confidence in disease freedom, whereas active testing alone is unlikely to detect outbreaks in time. Farmer reporting is central to such systems; behavioural studies in France show that financial compensation, awareness of reporting objectives, and participatory education strongly influence whether and how quickly farmers notify unexplained mortalities, directly affecting early-warning performance. New molecular and environmental tools expand early-warning capacity. Suites of droplet digital PCR assays enable high-resolution, simultaneous quantification of multiple oyster-relevant pathogens in farm-proximal waters, revealing spatiotemporal hotspots where mortality risk increases and allowing farmers to adjust practices as pathogen loads rise. In parallel, temperature-based outlooks and spatial risk maps that integrate sea-temperature thresholds, turbidity and terrestrial inputs can guide targeted surveillance and proactive management of marine diseases, illustrating how environmental monitoring can be coupled with aquaculture health systems as oceans warm.

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