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Research Insight

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Effects of Different Stocking Densities on the Growth Performance and Survival of Zhikong Scallop (*Chlamys farreri*)

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Abstract Stocking density is a key ecological and managerial factor influencing the performance and sustainability of bivalve aquaculture. This study investigated the effects of different stocking densities on the growth performance and survival rate of *Chlamys farreri* under controlled culture conditions. A gradient of stocking densities was established to evaluate variations in shell growth, body weight gain, specific growth rate, and survival dynamics. Results indicated that stocking density significantly affected both growth performance and survival outcomes. Moderate density treatments generally promoted optimal growth by balancing resource availability and metabolic demand, while excessively high densities led to reduced growth rates, likely due to intensified competition for food, decreased water exchange efficiency, and increased accumulation of metabolic wastes. Survival rates exhibited a declining trend with increasing density, with density-induced stress and susceptibility to disease identified as key contributing factors. Environmental parameters such as dissolved oxygen and particulate food availability further modulated density-dependent responses. A case-based comparison across different aquaculture systems highlighted the importance of adaptive density management strategies in improving production efficiency. Overall, the findings suggest that optimizing stocking density is essential for maximizing growth performance and ensuring high survival rates in *Chlamys farreri* aquaculture, providing practical implications for sustainable shellfish farming.

Keywords Stocking density; *Chlamys farreri*; Growth performance; Survival rate; Aquaculture management

1 Introduction

Zhikong scallop (*Chlamys farreri*) is an economically important cultured bivalve in northern China and a major contributor to regional shellfish aquaculture because of its high nutritional value and well-developed adductor muscle (Wang et al., 2023). The species is naturally distributed along the coasts of northern China, Korea, and Japan, and its commercial value has supported the expansion of suspended culture systems in multiple coastal regions. In scallop aquaculture, stocking density is a core husbandry factor because it directly shapes individual growth, survival, physiological condition, and final farm yield. Earlier work on *C. farreri* in Korea showed a clear negative correlation between stocking density and shell growth, while survival was highest at the lowest density treatment of 20 individuals per compartment. Similar density-dependent responses have been reported across other scallop species, where growth commonly declines as density increases, although survival does not always respond identically across species and production systems. For *C. farreri* specifically, the scientific problem is not simply whether density matters, but how density interacts with food supply, hydrodynamics, temperature, and seasonal physiology to alter growth performance and mortality risk. A depletion model from Sungo Bay showed that rearing density, food concentration, and water movement interact at the farm scale, and that a density of 50 ind m⁻³ could reduce growth from 0% to 100% when current velocity was low, indicating that density effects depend strongly on local carrying capacity. Semi-field experiments in Sishili Bay further demonstrated that increasing *C. farreri* density can deplete seston through intense filtration and biodeposition, thereby impairing scallop growth in a limited water column. Temperature adds another layer of complexity, because scallop growth and mortality are often amplified by warm conditions; in sea scallops, density effects were most pronounced during summer, and low-density nets performed better within favorable thermal windows. This framework is especially relevant for *C. farreri*, whose summer mortality episodes in China have long suggested that density-dependent stress operates together with reproductive load and environmental deterioration. Since 1996, mass summer mortalities have occurred in most

northern Chinese farming areas, with cumulative mortality reaching 85%-90% in some sites, and medium- and high-density groups showing faster early mortality and reduced growth. Earlier analyses likewise argued that long-term continuous high stocking density can worsen environmental aging, food shortage, self-pollution, and pathogen proliferation during summer, thereby reducing the tolerance of cultured scallops. More recent studies in other cultured scallops also indicate that overcrowding can suppress immune function and increase bacterial vulnerability, suggesting that density affects not only space competition but also health resilience (Feng et al., 2023).

The aquaculture industry of *C. farreri* has developed from a seed-dependent coastal practice into a large and regionally dominant mariculture sector. Once abundant and reliable seed supply became available, *C. farreri* culture expanded rapidly, and by 1985 cultured yield had already exceeded the wild fishery in Shandong Province. Nursery and grow-out technologies based on nets, cages, and other suspended devices enabled large-scale farming, with conventional cages holding 30-50 scallops per compartment and 450-600 cages per hectare. In Sungo Bay, one of the representative production centers, scallop longline culture has been estimated to exceed 50,000 tonnes annually, making site selection and suitable rearing density key management issues. Over the past decades, however, the industry has faced a transition from simple expansion toward quality-oriented and sustainability-oriented development, because overexploitation has been associated with reduced shellfish growth and increased disease incidence. Field trials have shown that culture location matters as much as density: in Sungo Bay, offshore longline systems produced higher survival than inshore systems, and offshore densities of 20-30 individuals per disc achieved better shell and tissue growth than denser treatments, likely because stronger currents improved food delivery. Seasonal culture performance also remains uneven, as *C. farreri* in deep water of Haizhou Bay grew rapidly except in summer, while most mortality occurred during the first summer and autumn. These production challenges have stimulated broader interest in improved farming modes, including offshore culture, integrated multi-trophic aquaculture, and germplasm improvement. Offshore studies indicate that *C. farreri* can maintain continuous growth in new farming spaces such as offshore wind farm areas, although growth may remain below that observed in more favorable reference sites and temperature appears to be a key determinant (Lee et al., 2023). Integrated culture with *Gracilaria lemaneiformis* has shown strong nutrient removal capacity, with ammonium and phosphorus reduction efficiencies reaching 83.7% and 70.4%, respectively, indicating that system optimization can improve environmental performance around scallop farming. At the same time, the industry is paying closer attention to product quality, food safety, and genetic improvement: recent surveys across the Shandong Peninsula evaluated nearly 70 hazard indicators and 90 nutritional and flavor substances in cultured *C. farreri* (Song et al., 2023), while genomic analyses found high genetic diversity in natural populations and identified selected strains with growth- and stress-resistance-related signatures that could support future breeding programs. Seasonal monitoring has also shown that some metal-related consumer risks, especially cadmium and arsenic, still require attention in risk assessment even when seawater concentrations remain below regulatory limits.

Against this background, the present study focuses on a central practical and scientific question: what stocking density best balances growth performance and survival in cultured Zhikong scallop under suspended farming conditions? This question is important because prior studies consistently show that low density tends to favor individual growth, but the optimal density for production depends on species, life stage, environment, and management objectives. Even larval and hatchery studies in other scallops show that density effects are not biologically trivial and can shift according to water exchange, developmental stage, and the trade-off between growth, survival, and space efficiency. Therefore, evaluating density responses in *C. farreri* under explicit farming conditions is necessary for converting broad principles into species-specific recommendations. The objective of this study is to compare the growth performance and survival of *C. farreri* cultured at different stocking densities, and to identify a density range that can improve biological performance while supporting efficient farm management. Its innovation lies first in linking a classic husbandry variable to the current needs of the *C. farreri* industry, which now requires not only high output but also lower mortality, better environmental matching, and more stable product quality. Its second significance is that density optimization can provide a simple and directly applicable management tool for reducing food competition, minimizing stress accumulation, and lowering summer mortality risk in commercial culture. Its third significance is that the results can contribute to site-specific and system-specific

refinement of scallop farming, complementing carrying-capacity modeling, offshore expansion, and ecological integration strategies already proposed for this species. In addition, because suspension-cultured scallops strongly influence seston removal, nutrient flux, and benthic-pelagic coupling, selecting an appropriate density also has ecological implications beyond individual growth alone. Overall, studying the effects of different stocking densities on the growth and survival of *C. farreri* is both theoretically meaningful and practically urgent, because it addresses the intersection of animal performance, environmental capacity, and sustainable industry development.

2 Physiological and Ecological Basis of Growth and Development in *Chlamys farreri*

2.1 Filter-feeding mechanisms and energy acquisition pathways

As a suspension-feeding bivalve, *Chlamys farreri* acquires energy by filtering mixed seston from the water column and regulating particle capture, selection, ingestion, and absorption in response to rapidly changing environmental conditions. A functional culture model showed that the species can differentially process phytoplankton, non-phytoplankton organic matter, and inorganic particles through gill retention and pre-ingestive rejection in pseudofeces, indicating that energy intake depends on both food quantity and particle quality rather than chlorophyll alone (Hawkins et al., 2002). This is ecologically important because living phytoplankton contributed less than 20% of suspended particulate organic matter in Sungo Bay, so a substantial fraction of assimilable energy must come from non-phytoplankton organic particles with highly variable energy content.

Feeding performance is further constrained by the interaction between seston structure and environmental temperature. Clearance rate in *C. farreri* varies over an order of magnitude and follows a unimodal response to total particulate volume and chlorophyll concentration, peaking before declining at excessive seston loads, which indicates flexible but capacity-limited feeding regulation (Hawkins et al., 2001). Laboratory energetics experiments likewise showed that filter-feeding rate increases with water temperature and body weight under appropriate thermal conditions, reaches a maximum at about 23°C, and then declines, while assimilation efficiency falls as algal concentration rises, suggesting a trade-off between rapid particle processing and digestive efficiency.

2.2 Growth regulation and metabolic allocation characteristics

Growth in *C. farreri* depends not only on how much energy is acquired, but also on how that energy is partitioned among shell formation, soft tissue growth, maintenance metabolism, and excretion. Multi-tissue metabolomic evidence indicates that growth-associated pathways are distributed across mantle, gill, adductor muscle, and digestive gland, with shared roles for sphingolipid metabolism, fatty acid biosynthesis, and transport processes, while tissue-specific pathways support shell deposition, nutrient absorption, and muscle development (Zhang et al., 2024). Within this system, the gill is especially important because it functions as the primary feeding tissue, initiates nutrient absorption, and helps maintain physiological equilibrium across other soft tissues (Figure 1).

Energy-budget studies show that metabolic allocation changes systematically with temperature and body size, which helps explain density-dependent variation in growth potential. Between 8 and 18°C, respiration, ammonia excretion, and ingestion all increase with rising temperature, but respiration and ingestion peak at 23°C and decline at 28°C, indicating that thermal elevation does not indefinitely promote production. Body size is another key determinant of allocation, because the proportion of energy lost to respiration increases as scallops grow, while the fraction deposited into growth declines; under simulated natural seston conditions, respiration accounted for 42.2%-51.7% of intake, whereas only 12.7%-21.7% was retained for growth.

2.3 Mechanisms of environmental stress response

Environmental stress in *C. farreri* is expressed through coupled metabolic, oxidative, immune, and behavioral responses, with temperature being one of the most important drivers. Metabolomic analysis under 27°C heat stress showed broad shifts in amino acid, carbohydrate, lipid, and nucleotide metabolism, and decreases in pyruvic acid together with increases in citric and fumaric acid indicated altered energy metabolism aimed at sustaining ATP supply during thermal challenge (Dong et al., 2022). Heat exposure also induced oxidative stress, but increased total antioxidant capacity in gill and mantle tissues suggests that the scallop retains some adaptive capacity through antioxidant regulation rather than passive injury alone.

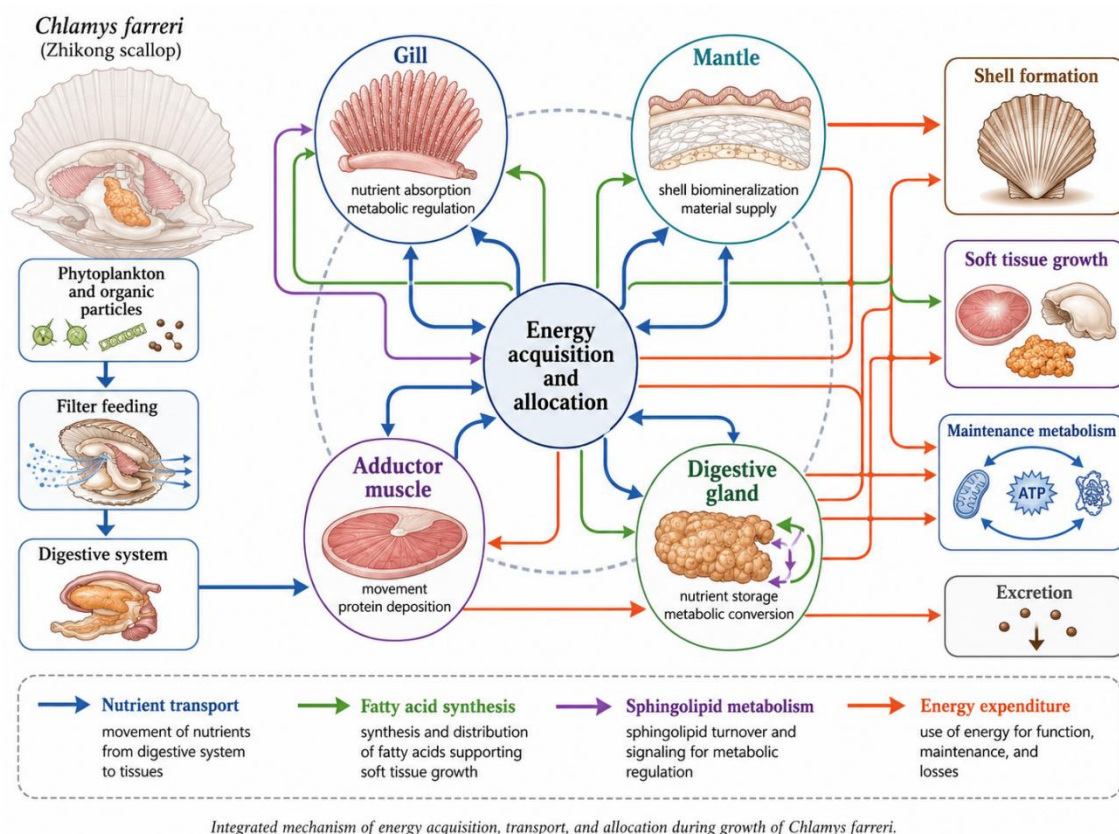


Figure 1 Conceptual model of energy acquisition, tissue-specific metabolism, and growth allocation in *Chlamys farreri*. Energy obtained from filtration feeding is distributed among shell formation, soft tissue growth, maintenance metabolism, and excretion through coordinated functions of the gill, mantle, digestive gland, and adductor muscle

This compensatory capacity has clear limits when stress becomes acute, combined, or prolonged. Under high temperature and *Vibrio anguillarum* challenge, glycogen reserves declined rapidly, cellular energy allocation fell, and the combined stress imposed greater energetic costs than either factor alone, supporting the view that summer mortality can arise from energy being diverted from growth toward defense and repair (Wang et al., 2012). Oxygen limitation produces a similar breakdown in performance: dissolved oxygen below 4.5 mg/L reduced survival and depressed immune responses, while separate hypoxia experiments estimated an LC50 of 1.8 mg/L and linked rising mortality to disrupted metabolic homeostasis despite depressed respiration and escape-related activity (Li et al., 2019). Overall, the growth and survival of *Chlamys farreri* are governed by a tightly linked physiological system in which feeding plasticity, metabolic allocation, and stress tolerance jointly determine production outcomes. This physiological and ecological framework directly supports the study of stocking density, because density can alter food availability, metabolic demand, and exposure to thermal or hypoxic stress that ultimately shape scallop growth performance and survival.

3 Ecological Drivers of Stocking Density Variation

3.1 Interspecific and intraspecific competition

In suspended culture systems, the first ecological constraint on stocking density is competition for limited food particles within and around the culture unit. Across scallop farming studies, growth declines consistently as stocking density increases, and comparative analyses indicate that this effect is mainly driven by reduced access to suspended food rather than by density alone as an abstract crowding variable. Experimental work that separated living scallops from space-occupying dummies showed that growth fell sharply when density was increased with real animals, but not when space was filled by non-feeding dummies, demonstrating that food depletion is the principal mechanism behind density-dependent growth reduction in suspended scallop culture.

Space limitation still matters, but it usually acts as a secondary constraint that amplifies feeding interference once individuals become larger or shell contact becomes frequent. Meta-analysis of net-cultured sea scallops found that shell contact can inhibit feeding and that relative growth rate decreased by about 55% as areal coverage increased from 1% to 50%, showing that physical crowding can intensify the ecological effects of food competition. Similar patterns have been reported in other bivalves, where increasing body size raises both food demand and space demand, so density effects often become more apparent later in the culture cycle rather than immediately after stocking.

3.2 Water exchange and local microenvironment changes

Stocking density also alters the hydrodynamic and chemical microenvironment experienced by cultured scallops because dense culture structures slow water movement and reduce the renewal of food and oxygen inside the culture unit. An ecosystem model for a kelp-bivalve bay showed that aquaculture structures can significantly weaken water-exchange capacity, increasing half-exchange duration from about 7 days without aquaculture to about 16 days with culture present, which means that high-density farming can modify local flushing at the bay scale (Liu et al., 2025). At the operational scale, water-exchange experiments in scallop larviculture further showed that higher exchange rates improved larval yield and allowed high densities to be maintained more effectively, indicating that the ecological impact of density depends strongly on the rate at which the surrounding water is renewed (Sühnel et al., 2024).

These hydrodynamic effects are important because they shape food delivery, metabolic waste dilution, and local oxygen conditions simultaneously. In sea scallop culture, current speed was identified as an important factor in food delivery, although excessively strong flow can also inhibit filtration, so the relationship between density and performance depends on whether local flow supports or restricts seston replenishment. Evidence from broader intensive aquaculture systems points in the same direction: as stocking density rises, dissolved oxygen tends to fall while ammonia rises, showing that inadequate water renewal converts density stress into a local microenvironment problem rather than a simple numerical one (Firayani, 2024).

3.3 Waste accumulation and ecological feedback effects

A third ecological driver of stocking density variation is the accumulation of feces, pseudofeces, and other biodeposits generated by dense populations of filter feeders. In *Chlamys farreri* culture, filtering and biodeposition can greatly enhance the transfer of suspended matter, carbon, nitrogen, and phosphorus from the water column to the seabed, and sedimentation rates at culture sites have been measured at about 2.46 times those at reference sites (Zhou et al., 2006). This means that higher stocking densities do not simply increase production; they also strengthen benthic-pelagic coupling, changing the ecological context in which scallops themselves continue to feed and grow.

These feedbacks can be beneficial at moderate intensity but harmful when organic loading exceeds local assimilative capacity. On one hand, suspended bivalve culture can function as a biofilter and help mitigate eutrophication by removing seston from nutrient-enriched waters. On the other hand, field and mesocosm studies of bivalve biodeposition show that increasing farm density promotes organic matter accumulation, anoxic sediment development, and reduced benthic infaunal abundance, while species-specific biodeposit reactivity can also elevate dissolved inorganic carbon and ammonium production during decomposition (Murphy et al., 2019; Lavoie et al., 2024). Overall, variation in optimal stocking density for *Chlamys farreri* is controlled by the interaction of competition, water exchange, and waste feedbacks. For this species, density should therefore be understood as an ecological threshold problem: once food depletion, reduced flushing, and biodeposition accumulation exceed local carrying capacity, scallop growth and survival begin to decline.

4 Experimental Design and Rationale for Density Gradients

4.1 Principles for setting stocking density gradients

Stocking density gradients should be set to span a real biological contrast rather than only small numerical differences, because scallop growth usually declines progressively as density increases. Gradient levels should also reflect practical culture ranges used in scallop farming experiments, such as the six-density design from 136 to 818 spat m⁻² used in juvenile giant scallops, which allowed growth, yield, and survival to be compared across a broad

husbandry spectrum. For *C. farreri*, this logic supports using low, medium, and high density treatments that are clearly separated and still relevant to suspended production systems. Methodological rigor also requires minimizing size-related bias, because variation in initial body size can distort estimates of survivorship, yield, and the apparent optimum density if groups are not comparable at the start.

Density levels should be chosen with reference to both competition mechanisms and production goals. Semi-field work on *C. farreri* showed that increasing scallop density in a limited water column depleted seston and impaired growth, so the upper gradient should be high enough to test food limitation explicitly. At the same time, some scallop studies show that the commercially useful density is not always the density that maximizes individual growth, because optimal density depends on product size, grow-out strategy, and transfer timing. This is why the gradient should be designed not only to test whether low density grows faster, but also to identify a density range that balances shell growth, soft-tissue gain, survival, and unit-area output. A stepwise or staged density concept can also be justified, since larval studies found that production efficiency improved when density was reduced as animals developed and space demand increased (Mazón-Suástegui et al., 2022).

4.2 Experimental system and culture unit configuration

The experimental system should use a standardized suspended culture unit so that density is the main intentional variable. A strong design model is the semi-in situ flow-through seawater system used for *C. farreri*, which maintained continuous exchange with natural bay water while allowing density-dependent changes in seston, filtration, and biodeposition to be measured under controlled conditions. For grow-out trials, lantern-net or disc-based suspended units are appropriate because they match commercial farming practice and have already been used successfully to compare initial densities of *C. farreri* in inshore and offshore settings (Zhang et al., 2011). Unit dimensions, mesh size, layer number, and scallop number per layer should remain constant within each treatment series so that the experiment tests density rather than enclosure design.

Configuration should also account for space occupancy and water renewal inside each unit. Sea scallop work recommends keeping low-density nets below about 33% areal coverage, because growth in such nets did not decline during summer or fall from density effects alone. In *C. farreri*, a suspended culture design of eight-layer lantern nets with 30-cm diameter and 20-cm height per layer has been used in a one-year field study, providing a realistic reference for layer-based unit construction and stocking calculations. Experimental units should therefore be configured so that the low-density treatment remains clearly below crowding thresholds, while higher treatments approach levels at which food depletion and shell contact are more likely. Replication is also essential, and density experiments in scallops commonly use triplicate or higher replication to separate treatment effects from unit-level variability (Sühnel et al., 2024).

4.3 Experimental duration and process control considerations

Experimental duration should be long enough to capture growth trajectories and delayed mortality, not just short-term acclimation. Short trials can detect acute physiological responses, but density-dependent effects on growth and survival often emerge over months; for example, a *C. farreri* offshore study ran from May 2007 to March 2008 and showed that market size was reached after 10 months, with density effects expressed across seasonal growth peaks (Zhang et al., 2011). A one-year design is especially useful for this species because summer is a critical period when high temperature coincides with lower growth and higher mortality risk. If a full annual cycle is not feasible, the experiment should at minimum include the main warm season when density stress is most likely to be amplified.

Process control should include regular monitoring of water quality and animal condition throughout the trial. Previous *C. farreri* experiments measured temperature, salinity, current speed, chlorophyll a, and total particulate material concurrently with growth and survival, which provides the environmental context needed to interpret density responses mechanistically. Dissolved oxygen deserves specific attention because exposure below 4.5 mg/L reduced survival and depressed immune responses in *C. farreri* within 21 days. Sampling should therefore include periodic measurements of shell height, soft-tissue or muscle weight, and survival, while handling frequency should be minimized because transfer and repeated measurement can themselves elevate mortality in scallop stocking

experiments. From a practical standpoint, the schedule should also avoid unnecessary thinning during periods of high thermal stress, since proactive low-density stocking in spring has been recommended to reduce summer handling risk. In sum, the rationale for density-gradient design in *Chlamys farreri* is to test a broad but realistic range of crowding levels under standardized suspended culture, with sufficient duration and environmental control to reveal how density affects both growth performance and survival.

5 Growth Performance Response Characteristics

5.1 Shell length and body weight growth dynamics

Stocking density shapes *Chlamys farreri* growth performance through three linked dimensions: shell and weight growth, specific growth and energy efficiency, and nonlinear threshold responses. The synthesis below follows that structure, keeps each subsection to two natural paragraphs, and limits each paragraph to no more than two distributed citations. Shell length and body weight growth in *Chlamys farreri* decline as stocking density increases, and this pattern has been observed directly in suspended culture. In a 16-month hanging-culture study in Korea, shell height and total weight after culture ranged from 64.35 to 76.23 mm and from 41.53 to 64.85 g across treatments, with growth negatively correlated with stocking density (Park et al., 2012). A field trial in Sungo Bay similarly found that offshore groups stocked at 20 and 30 individuals per disc achieved significantly greater shell height, soft-tissue weight, and muscle weight than denser groups, showing that lower or moderate density supports better somatic accumulation under favorable hydrodynamic conditions.

The same density effect appears across scallop and other suspended bivalve systems, which strengthens the biological interpretation of the *C. farreri* pattern. In juvenile giant scallops, shell height growth at 25-50 scallops per net was nearly twice that observed at 200-250 scallops per net, and dry mass of shell, muscle, and other soft tissues also declined at higher densities. In suspended mussel culture, individuals reared at lower densities reached greater final length and weight than those at higher densities, indicating that reduced competition allows body-size divergence to widen over time rather than remain constant (Cubillo et al., 2012).

5.2 Specific growth rate and growth efficiency differences

Specific growth rate shows the same general decline with increasing density, but the response often varies by culture stage and subsequent rearing conditions. In *Nodipecten nodosus*, intermediate-phase scallops held at 50 m⁻² had significantly higher shell height, survival, and specific growth rate than scallops reared at 800-3200 m⁻², indicating that crowding suppresses early growth velocity (Garcia et al., 2022). Yet after all groups were later reduced to the same low density, scallops originating from high-density treatments showed increased SGR at the beginning of grow-out, suggesting that part of the early growth suppression can be followed by compensatory growth when competitive pressure is relieved.

Growth efficiency differences also reflect how assimilated energy is partitioned under density-related stress rather than growth rate alone. Dynamic Energy Budget comparisons across bivalves indicate that scallops tend to combine rapid growth with relatively low production efficiency, meaning that fast structural gain can come at a higher energetic cost than in slower-growing species (Lanjouw et al., 2024). At the physiological level, growth variation within *C. farreri* is associated with large differences in body weight, soft tissue weight, and muscle weight between fast- and slow-growing individuals, together with metabolite patterns linked to fatty acid biosynthesis, sphingolipid metabolism, and transport pathways, which implies that density effects on SGR likely operate through altered metabolic allocation as well as reduced feeding opportunity (Zhang et al., 2024).

5.3 Nonlinear response patterns to stocking density

The response of growth to stocking density is not strictly linear, because density interacts with temperature, current speed, and local food renewal to create threshold-like declines. A meta-analysis of net-cultured sea scallops found that stocking density was one of the strongest negative determinants of growth, and increasing areal coverage from 1% to 50% reduced relative growth rate by about 55%. A separate field study showed that growth responses to density were nonlinear across sites and seasons, with optimal shell growth concentrated in a 10°C-15°C window and density effects becoming especially pronounced during summer.

For *C. farreri*, nonlinear density effects are especially evident when food depletion and hydrodynamics are considered together. A depletion model for Sungo Bay predicted that at 50 ind m⁻³, density could reduce growth anywhere from 0% to 100% depending on current velocity below 20 cm/s, which means the same nominal density can be either tolerable or strongly growth-limiting depending on local flow. Carrying-capacity modeling in a Chinese bivalve culture bay likewise estimated that scallop capacity is seasonally low in spring and summer and proposed that mean-size scallop density should not exceed 59 ind m⁻², reinforcing the idea that the biologically acceptable density range is context dependent and bounded by seasonal ecological limits rather than by a single universal value (Liu et al., 2025). Overall, growth performance in *Chlamys farreri* responds to stocking density through reduced shell and tissue growth, lower specific growth under crowding, and nonlinear threshold effects shaped by environment. These response characteristics support using moderate or low density ranges in culture practice, especially where warming, weak flow, or food depletion increase the likelihood of growth suppression (Figure 2).

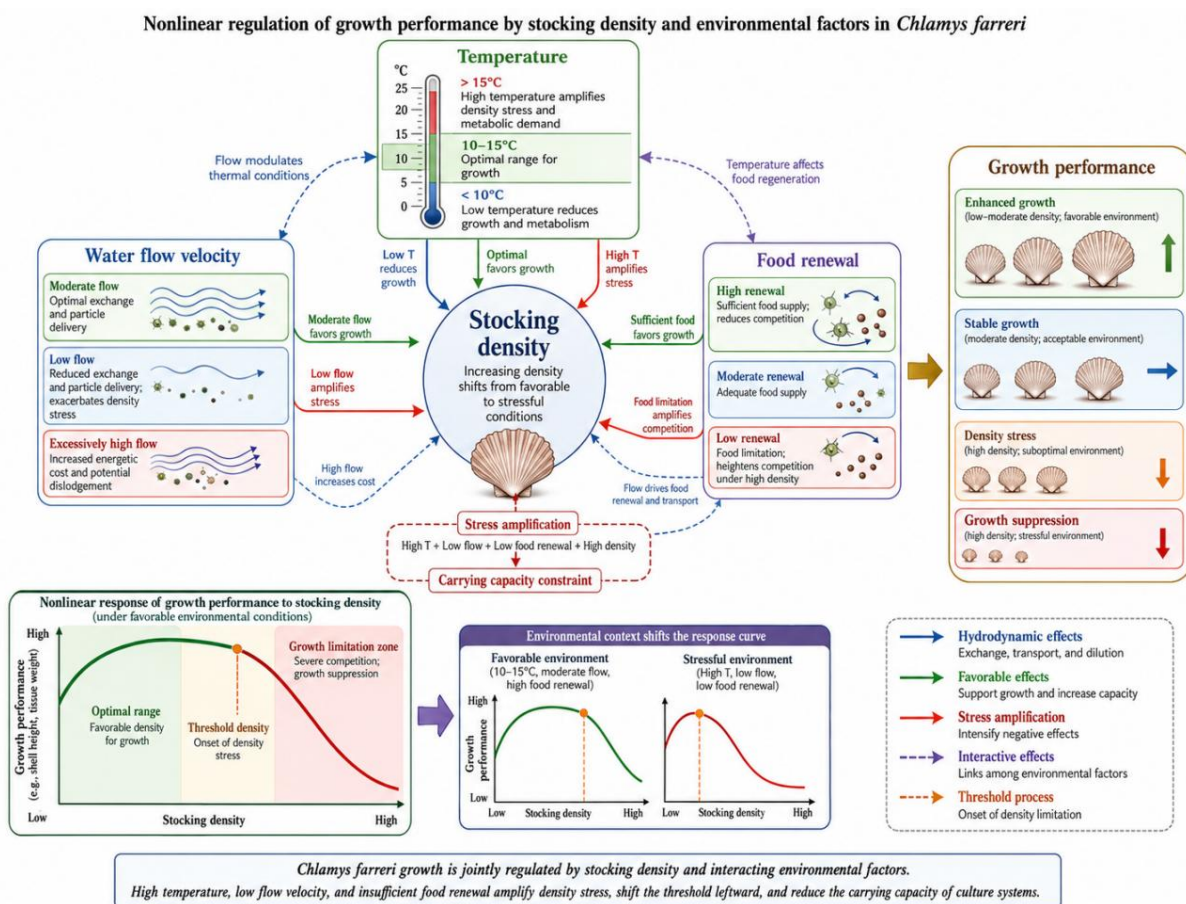


Figure 2 Conceptual framework illustrating the interactive effects of stocking density, temperature, hydrodynamics, and food availability on scallop growth. Environmental conditions modify density-dependent responses by regulating food renewal, metabolic demand, and ecological thresholds

6 Survival Rate Variation and Influencing Factors

6.1 Identification of mortality patterns under density stress

In *Chlamys farreri*, mortality under density stress is strongly seasonal rather than uniform across the culture cycle. A large field study in northern China found that most deaths occurred in July and August, during the later spawning season when water temperature reached 23°C–26°C, and cumulative mortality eventually reached 85%–90% across sites. A separate hanging-culture study in Korea also showed that mortality clustered in March–April and September–October rather than increasing steadily through time, indicating that density-related loss emerges in seasonal pulses linked to changing environmental and physiological conditions (Park et al., 2012).

Density mainly changes the timing and intensity of mortality onset. In the Chinese summer-mortality study, medium- and high-density groups had higher initial death rates than low-density groups, even though all density groups ultimately experienced severe losses. In Korea, survival ranged from 82% to 100% and declined as stocking density increased, with the highest survival at 20 individuals per compartment. Similar cross-species evidence shows that density is often a weak predictor of mortality at low or moderate crowding but becomes important at very high densities, especially when net coverage exceeds practical limits.

6.2 Disease risk and immune stress responses

High stocking density appears to increase disease risk by weakening immune defense and raising microbial pressure. In noble scallops, high-density culture caused significantly higher mortality together with higher bacterial load, higher reactive oxygen species, and lower antibacterial capacity against *Vibrio parahaemolyticus*, indicating that overcrowding shifts scallops toward an oxidative and infection-prone state. A later study on the same species found that high-density groups had much lower survival than normal-density groups and significantly lower expression of CnMyD88, with weaker post-challenge immune expression after *Vibrio* exposure, supporting density-induced immunosuppression at the molecular level (Feng et al., 2023).

The likely mechanism in *C. farreri* is similarly multifactorial rather than attributable to a single pathogen. During mass mortality events, histological observations detected ciliates, larvae of other organisms, and abnormal secretions in the gill cavity, but prokaryotic inclusion bodies showed low prevalence and no clear correlation with deaths, arguing against one dominant infectious cause. More broadly in bivalves, reproduction and post-spawning stress depress haemocyte function, and in scallops granulocyte proportion drops in summer and early autumn around reproduction completion, which provides a physiological basis for the coincidence of density stress, weakened immunity, and seasonal mortality (De La Ballina et al., 2022).

6.3 Determination of optimal survival density threshold

The evidence does not support a single universal survival density for *C. farreri*; instead, the threshold depends on season, unit design, and local carrying capacity. In Jiaozhou Bay, ecological assessment concluded that current scallop culture was saturated and mortality was high, leading to a recommended density reduction to 280 individuals per cage. The same analysis cited earlier field observations that mortality stayed around 5% at ≤ 50 individuals per layer but increased significantly above that threshold, with some years reaching 90% mortality under heavier stocking (Liu et al., 2021).

Field comparisons suggest that a low-to-moderate density window is most defensible for survival-oriented culture. Offshore *C. farreri* culture in Sungo Bay showed that survival was inversely proportional to initial density, while offshore conditions improved outcomes relative to inshore sites because stronger currents likely improved food supply and local flushing. Modeling studies reinforce that density thresholds should be tied to carrying capacity rather than fixed numerically across all farms: scallop carrying capacity is lowest in spring and summer in culture bays, and mean-size scallop density in Sanggou Bay was estimated not to exceed 59 ind m^{-2} (Liu et al., 2025). Overall, for *Chlamys farreri*, optimal survival density is best defined as the highest density that remains below seasonal crowding, warming, and water-exchange limits, rather than as a single constant stocking number.

7 Coupling Relationship Between Water Environment Regulation and Density Effects

7.1 Dissolved oxygen consumption and supply limitations

Stocking density affects dissolved oxygen by changing both biological demand and the rate at which oxygenated water is renewed around cultured scallops. In intensive aquaculture systems, the reduction in dissolved oxygen increases with stocking density and is alleviated by stronger current speed, indicating that oxygen stress is fundamentally a coupled effect of biomass load and water exchange (Wen et al., 2025). This interaction is consistent with ecological carrying-capacity analyses in Chinese bivalve farming areas, where carrying capacity was regulated mainly by filtration rate and temperature, and summer-autumn conditions were identified as the period of lowest scallop carrying capacity.

For scallops, oxygen limitation also suppresses energy acquisition and survival rather than acting only as a background water-quality variable. In northern bay scallops, hypoxia reduced algal clearance by 88%, and the combination of hypoxia with high temperature reduced clearance by 97%, showing that low oxygen can sharply constrain feeding performance (Tomasetti et al., 2023). Dynamic Energy Budget modeling in *Argopecten purpuratus* likewise showed that the negative effects of hypoxia on growth and reproduction were explained by decreased assimilation and reserve mobilization, while severe summer events were better explained when additional maintenance costs were imposed by sulfide-associated stress.

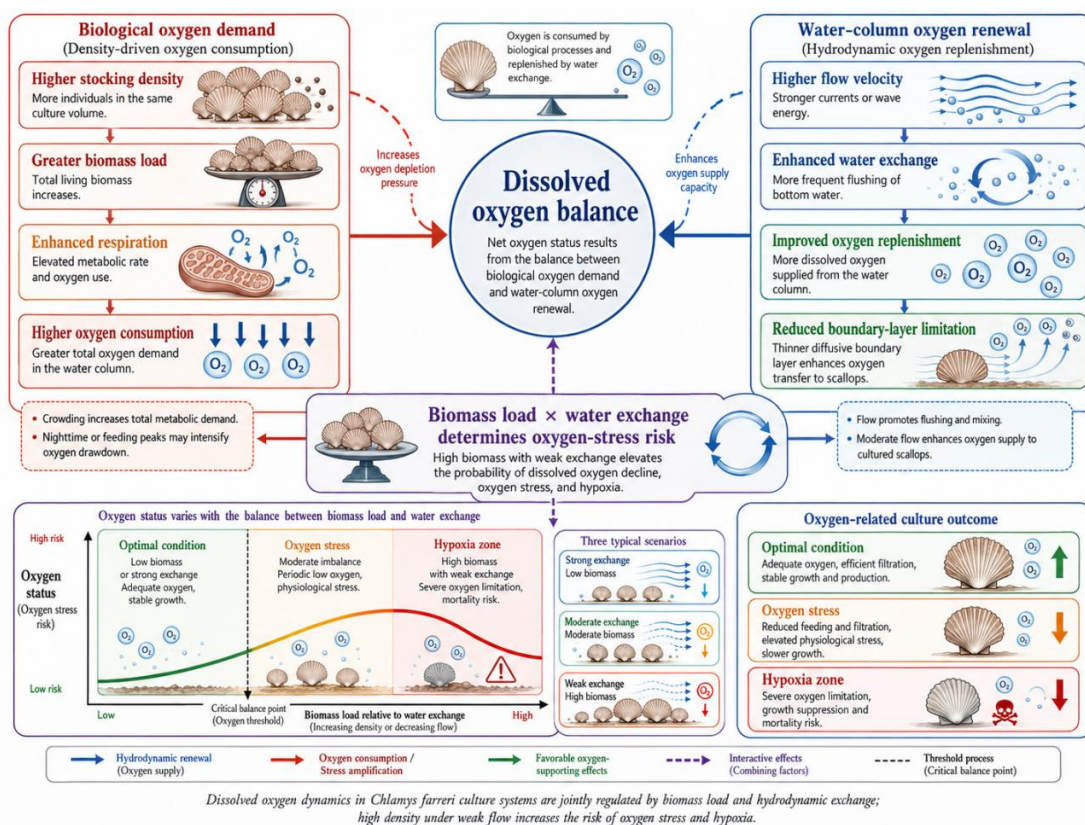


Figure 3 Conceptual model illustrating the coupled effects of stocking density and water exchange on dissolved oxygen dynamics in scallop aquaculture systems. Oxygen availability is determined by the balance between biological oxygen demand and hydrodynamic oxygen renewal

7.2 Changes in feed resource utilization efficiency

The effect of stocking density on feed resource utilization in *C. farreri* is mediated chiefly through seston depletion and density-dependent changes in filtration. A semi-in situ experiment in Sishili Bay showed that the presence of scallops strongly reduced seston and chlorophyll *a* in the water column, and increasing density in a limited water mass caused seston depletion that impaired scallop growth. The same study found that both filtration rate and biodeposition rate were negatively correlated with scallop density but positively related to seston concentration, indicating that crowding lowers the per-capita efficiency of resource capture as local food becomes depleted.

This density effect is nonlinear because feeding efficiency depends not only on food amount but also on hydrodynamics and seston structure. A depletion model for Sungo Bay predicted that at 50 ind·m⁻³, density could reduce scallop growth by anywhere from 0% to 100% when current velocity was below 20 cm/s, which shows that identical stocking levels can have very different nutritional consequences under different flow regimes (Bacher et al., 2003). At the physiological level, clearance rate in *C. farreri* follows a unimodal response to particle volume and chlorophyll concentration, peaking at about 7.1 l·h⁻¹·g⁻¹ when seston volume was 2.0 mm³/L and chlorophyll *a* was 5.3 µg/L before declining at higher concentrations, so excessive suspended load does not continuously improve food use.

7.3 Evolution of sediment conditions and micro-ecosystems

Higher stocking density modifies the benthic environment by increasing biodeposition and strengthening pelagic-benthic coupling. In *C. farreri* culture, daily biodeposit production in early summer was estimated at $7.78 \text{ g} \cdot \text{m}^{-2}$, with associated carbon, nitrogen, and phosphorus transfer to the benthos, indicating a substantial enhancement of material flux from the water column to sediments. This process is ecologically significant because concentrated bivalve biomass can generate intense particulate organic matter deposition on surrounding sediments, even though the local impact depends on subsequent resuspension and transport.

Sediment responses then feed back to the culture environment through oxygen demand, nutrient release, and microbial restructuring. In a coastal scallop farming area affected by summer hypoxia, sediment in the mariculture zone showed higher oxygen consumption than non-mariculture sediment, supporting a direct link between scallop biodeposition and dissolved oxygen loss in overlying water. Bivalve-related bioturbation can also shift sediment microbial function: moderate clam density increased nitrogen-cycling activity and the abundance of related genes in IMTA sediment, whereas bivalve culture in another IMTA system was associated with higher dissolved oxygen, lower ammonia and nitrite, and more nitrifying and denitrifying bacteria in the bivalve area (Yuan et al., 2022; Kong et al., 2023). Overall, the density effect in *Chlamys farreri* is inseparable from water-environment regulation: higher density elevates oxygen demand, intensifies food depletion, and accelerates biodeposition, while water exchange and sediment processing determine whether those pressures remain tolerable or become growth- and survival-limiting.

8 Case Study: Density Optimization Practices in Different Aquaculture Systems

8.1 Density optimization in offshore raft culture systems

Offshore raft or suspended longline systems optimize stocking density by using stronger water exchange to buffer competition, while still requiring density restraint to maintain growth and survival. In *Chlamys farreri*, offshore culture in Sungan Bay produced higher growth and survival than inshore culture, and the best offshore performance occurred at 20-30 individuals per disc, which was attributed to higher current speed and improved food supply. This aligns with broader suspended-culture evidence showing that low net coverage and favorable temperature windows improve shell growth and survival, with recommended stocking below about 33% coverage and preference for bay mouths or estuarine mouths where physical conditions are more favorable. The practical rationale for lower offshore densities is not only biological but also operational. Meta-analysis across Northwest Atlantic scallop farms found that stocking density was the second most important determinant of growth and its effect was consistently negative, indicating that even productive offshore systems cannot fully offset crowding penalties. At the farm scale, density optimization must also balance growth against labor and equipment costs, because low-density net stocking increases the number of nets that growers must service and therefore raises handling costs and infrastructure demand. For this reason, offshore density optimization is best treated as a compromise between maximizing individual growth and minimizing the spatial and economic costs of sparse stocking.

Offshore density control is also constrained by local hydrodynamic modification caused by the culture system itself. Modeling from Sungan Bay showed that high-density suspended aquaculture weakened current velocities in culture layers by about 65% in scallop zones and reduced bay-scale water-exchange ability, implying that excessive facility density can erode the flushing advantage that offshore sites initially provide (Liu and Zhang, 2022). Similar environmental comparisons in Japanese scallop farming showed that site suitability peaks were associated with current effects, whereas extreme summer temperatures above 24°C were linked to poor culture performance and mortality, reinforcing that offshore density targets must be adjusted to site-specific circulation and thermal regimes (Aura et al., 2016). A second offshore lesson is that commercially optimal density is not always the biologically lowest density. In juvenile sea scallops, maximum growth occurred at 50 scallops per net, but growth at 100 per net was only slightly lower and was considered commercially preferable, because a moderate increase in density improved space use without causing a major decline in performance. A similar pattern was reported for queen scallops in Galicia, where maximum growth occurred at 25 scallops per tray, yet 50-100 per tray was recommended on a commercial scale because growth losses remained small while output per unit system increased.

8.2 High-density management strategies in hatchery/nursery phases

During hatchery and nursery phases, density optimization relies less on simple density reduction and more on stage-specific control of water exchange, size grading, and timely thinning. In recirculating larviculture of *Nodipecten nodosus*, low density combined with high water exchange gave the highest survival and competent-larvae yield, whereas high density with high exchange produced the greatest total larval number per tank volume, showing that hatchery density can be raised if water renewal is strong enough to stabilize performance (Sühnel et al., 2024). In *Argopecten ventricosus*, early larval production was improved by starting at 6 larvae m/L and reducing density to 2 larvae m/L by day 7, indicating that high initial density can be useful if it is followed by planned thinning before crowding suppresses growth. Nursery systems also manage high density through unit configuration and animal redistribution rather than through a fixed low-density rule. In *Pecten fumatus* upwelling nurseries, growth declined progressively on downstream screens, but daily rotation of screen position eliminated much of this uneven growth and increased biomass gain, while the practical upper stocking limit for maintaining maximum growth was about 70% screen coverage. Land-based raceway nursery for *Pecten maximus* provided a different strategy: an intermediate nursery stage increased survival enough to offset roughly 20% higher operating cost, making denser and more controlled pre-sea rearing economically attractive when post-transfer losses are otherwise unstable.

Another common nursery strategy is to reduce the biological consequences of high density by controlling size structure and deployment method. In Catarina scallop longline culture, low density produced faster growth in nursery and intermediate phases, but homogeneous size selection at each stage helped standardize later performance and survival remained above 91% overall. In farm-based sea scallop nurseries, season, initial size, and gear type affected growth and recovery more strongly than the two collector-bag densities tested, showing that density management in early stages must be integrated with deployment timing and nursery design rather than treated in isolation. High-density nursery practice also carries a health cost if crowding is prolonged. In noble scallops, long-term overcrowding caused higher mortality, slower growth, higher bacterial load, and weaker antibacterial capacity, while a separate study showed lower survival and suppressed MyD88-related immune expression under high density (Liu et al., 2019). These results indicate that hatchery or nursery systems can use high densities temporarily, but only when exchange, handling, and duration are controlled tightly enough to prevent chronic stress from converting space efficiency into immunological risk (Feng et al., 2023).

8.3 Comparative analysis of density adaptation across different marine environments

Across different marine environments, density adaptation depends on how local food supply, current speed, temperature, and carrying capacity modify the cost of crowding. In Jiaozhou Bay, ecological modeling concluded that scallop stocks exceeded carrying capacity, that mortality rose significantly above about 50 individuals per layer, and that recommended density should be reduced to 280 individuals per cage. By contrast, in the offshore area of Sungo Bay, reducing *C. farreri* seeding density to around 20 individuals per layer was reported to improve both ecological conditions and culture efficiency, illustrating that optimal density becomes lower where the management goal includes ecosystem recovery as well as production (Liu et al., 2021). Temperature and depth further shift density tolerance across regions. In Galicia, queen scallop growth was lower at 2 m than at 7-12 m because surface waters had lower salinity in winter, higher summer temperatures, and lower chlorophyll a, showing that a nominal density can become suboptimal when vertical habitat quality declines. Bay scallop nursery studies likewise found that density effects depended on scallop size, with 16-17 mm juveniles tolerating up to 7500 m⁻² and 24-25 mm juveniles tolerating up to 2500 m⁻² without substantial growth reduction, so density standards should scale with body size rather than remain fixed through ontogeny.

Comparative evidence therefore supports an adaptive rather than universal density framework. Some systems can sustain relatively high densities with little survival penalty, as seen in giant scallops where survival remained 91% across 136-818 spat m⁻² and in sea-based nursery bags where two tested densities did not significantly alter recovery. Other systems are much less tolerant, especially when warming, poor flushing, or prolonged overcrowding interact, so density must be reduced proactively according to local environmental ceilings rather than only according to infrastructure capacity (Liu et al., 2021). Overall, density optimization in different aquaculture systems is not a

single technical rule but a context-dependent management strategy. For *Chlamys farreri*, the strongest case supports moderate offshore grow-out densities, staged control of early-life high density, and environment-specific adjustment based on hydrodynamics, seasonal temperature, and ecological carrying capacity.

9 Conclusions and Prospects for Practical Application

The central conclusion is that increasing stocking density generally reduces the growth performance of *Chlamys farreri*. In hanging culture, shell growth was negatively correlated with density and survival was highest at 20 individuals per compartment. Offshore longline culture in Sungo Bay likewise showed that scallops stocked at 20-30 individuals per disc achieved better shell and tissue growth than denser treatments, indicating that moderate density improves individual performance under commercially relevant conditions. The effect of density on survival is more conditional than its effect on growth, but the risk becomes pronounced when density stress overlaps with summer warming, reproduction, and poor circulation. Mass mortality studies in northern China found that most *C. farreri* deaths occurred in July and August at 23°C-26°C, and medium- and high-density groups showed faster initial mortality than low-density groups. This pattern is consistent with broader scallop evidence that density-related mortality and growth losses become strongest during warm seasons, when low-density culture is most protective.

In aquaculture practice, density optimization should begin with seasonal risk avoidance rather than with maximal short-term yield. Evidence from Jiaozhou Bay indicates that scallop culture density exceeded carrying capacity and should be reduced to 280 individuals per cage, while earlier field observations cited in that analysis reported low mortality at no more than 50 individuals per layer and improved ecological conditions when density in nearby Sungo Bay was reduced to 20 individuals per layer. These results support a management principle of keeping spring stocking low enough that thinning is unnecessary during summer stress periods. Site selection should be treated as part of density management, because the same nominal density can perform very differently across environments. A depletion model developed for Sungo Bay showed that at 50 ind m⁻³, density reduced growth from 0% to 100% depending on current velocity below 20 cm/s, showing that hydrodynamics directly determine whether crowding translates into food limitation. More generally, ecological carrying-capacity modeling across embayments has shown that local water circulation controls whether stocked biomass remains within precautionary limits, so lease placement in well-flushed areas should accompany density regulation.

The long-term prospect for sustainable bivalve aquaculture is favorable, but only if density control is integrated with ecosystem-based management. Ecological carrying capacity is best understood as the upper stocking level beyond which unacceptable environmental impacts appear, and its practical assessment must consider both production potential and ecological feedbacks. Recent indicator reviews further emphasize that carrying capacity differs among farm types and locations, so standardized but operational indicators are needed for management rather than relying on universal thresholds. Future development should therefore combine farm-scale optimization with bay-scale ecological planning, climate sensitivity, and habitat protection. In Sanggou Bay, aquaculture was modeled to reduce water-exchange ability substantially, and scallop carrying capacity was lowest in spring and summer, with mean-size density recommended not to exceed 59 ind m⁻². At the same time, sustainable expansion remains possible in some regions when ecosystem limits are respected, as shown by Yellow River Estuary modeling that found room for cautious future growth under current environmental conditions. Overall, the practical outlook for *Chlamys farreri* culture is strongest where moderate density, strong circulation, seasonal adjustment, and ecological carrying-capacity assessment are managed together.

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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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Effects of Different Feeding Regimes on Growth Performance of Mud Crab

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Abstract Feeding management is one of the most important factors influencing the growth performance, feed utilization, and economic efficiency of mud crab (*Scylla* spp.) aquaculture. This paper reviews the effects of different feeding regimes on mud crab growth performance by examining feeding frequency, feeding time, feeding level, feed type, and feeding strategy. Mud crabs exhibit unique growth characteristics associated with molting, which require precise nutritional support and feeding management. Appropriate feeding frequencies and multiple daily feeding events can improve weight gain, specific growth rate, feed conversion efficiency, and survival rate by enhancing feed intake and reducing nutrient loss. Feeding time also affects feeding behavior, with nighttime feeding generally showing advantages due to the nocturnal feeding habits of mud crabs. In addition, suitable feeding levels promote optimal growth and economic returns, whereas overfeeding and underfeeding may negatively affect water quality, feed efficiency, and crab health. The interaction between feed types and feeding strategies further influences production outcomes, with integrated approaches combining formulated feeds and fresh feeds often providing superior results. Case studies demonstrate that scheduled feeding, high-frequency low-quantity feeding, and intelligent precision-feeding systems can significantly enhance culture performance. Future research should focus on precision feeding technologies, automated monitoring systems, and sustainable feeding strategies to improve productivity and environmental sustainability in mud crab aquaculture.

Keywords Mud crab; Feeding regime; Growth performance; Feed utilization; Precision aquaculture

1 Introduction

Mud crab aquaculture has become an economically important coastal activity, and research increasingly treats feeding management as a central determinant of production efficiency, survival, and sustainability. *Scylla* species are among the most valuable commercially farmed crabs, with strong live-market demand across the Indo-Pacific and expanding trade in Asia and elsewhere (Paran et al., 2022). At the same time, the industry remains heterogeneous and only partly industrialized, spanning hatchery- and wild-sourced seed, extensive to intensive systems, and culture environments ranging from mangrove areas and ponds to cages and recirculating systems. This flexibility has helped the sector expand substantially in response to market demand and improvements in hatchery and grow-out technologies, especially across Southeast Asia, while also supporting food security, rural income, and broader coastal development (Diamahesa and Rahmadani, 2024). However, mud crab farming still faces persistent constraints, including dependence on wild seed, habitat degradation, disease risk, high production costs, and uneven technological adoption, all of which limit stable long-term growth. In some production regions, aquaculture still contributes only a small share of market supply, as shown in Bangladesh where about 95% of exportable crab reportedly comes from natural sources, underscoring the need for stronger nursery, hatchery, and farm-level innovations. Similar development tensions appear in East Africa and Kenya, where rising export demand, declining wild crab size, and pressure on mangrove ecosystems have driven interest in small-scale culture and silvofisheries as alternatives to capture-based supply. Even where the industry is profitable and technically straightforward, sustainable growth depends on improving seed production, feeding practices, and production management rather than continued reliance on wild resources alone.

Within this broader development context, feeding management is one of the most decisive operational factors in mud crab culture because it directly shapes growth rate, molting success, survival, feed conversion, water quality, and production cost. A recent synthesis of mud crab farming studies concludes that feed type, rearing system, and

stocking density jointly determine productivity and economic performance, with natural trash fish at around 15% of body weight often producing strong growth and feed efficiency during fattening. Feed is also economically critical because it represents a major share of operating costs, especially when high-protein ingredients are required, and this burden tends to increase as culture systems become more intensive. Empirical studies confirm that feed type matters: in juvenile and grow-out phases, some natural feeds such as trash fish or African land snail have produced better weight gain, feed conversion, and profitability than several alternatives (Andal et al., 2025). Formulated feeds also show promise under nursery conditions. In purple mud crab instars, commercial formulated feed outperformed minced fish in survival, growth, and feed conversion, suggesting that nutritionally balanced artificial diets can support more efficient early-stage culture. Likewise, in megalopa-to-crablet nursing of *S. paramamosain*, feed choice altered growth performance even when survival remained high across treatments, with Lansy pellets and frozen *Artemia* supporting better daily weight gain than pureed shrimp meat or NRD pellets. Beyond feed type, dose and schedule also influence outcomes. Different raw-fish feeding doses significantly affected absolute weight gain and specific growth rate in fattening *S. serrata*, with the best performance reported at the highest dose tested, while fresh-feed trials in single-room systems found that chicken intestine produced the best combination of growth, molting, and feed conversion among the tested diets. By contrast, not every feeding adjustment yields a strong biological response: in a recirculating aquaculture system, changing trash-fish feeding frequency from once to three times daily did not significantly affect growth or survival, although once-daily feeding produced the best observed performance (Mayzuri et al., 2025). These results show that feeding management is not a single-variable issue, but a composite of feed source, nutritional composition, ration size, and feeding frequency that interacts with production stage and culture system.

Against this background, research on different feeding modes is significant because the mud crab industry still lacks universally reliable, cost-effective, and species- or stage-specific feeding strategies. Although live foods such as rotifers and *Artemia* remain standard in hatchery production, they are expensive, nutritionally inconsistent, and insufficient for fully reliable mass seed production, which has motivated efforts to develop microbound and other formulated larval diets. Experimental work indicates that mud crab larvae and megalopae can respond differently to feeding modes across developmental stages: co-feeding microbound diet with *Artemia* improved zoea III survival and development relative to total replacement, whereas megalopae were able to ingest and develop on formulated particles with moderate survival depending on ingredient composition. Other studies similarly show that artificial feed supplementation is not always advantageous at every stage; for example, enriched *Artemia* alone remained sufficient for some larval stages of *S. tranquebarica*, while additional fresh or artificial feeds were more relevant closer to crablet production. In grow-out and fattening systems, the evidence also remains mixed rather than definitive. Some studies identify clear advantages for specific natural feeds such as trash fish, African land snail, or chicken intestine; others report that changing carbohydrate-to-lipid ratios in isoprotein artificial diets does not significantly alter molting, growth, or feed efficiency, despite slight performance trends among treatments. This variation suggests that optimal feeding regimes likely depend on crab species, life stage, rearing environment, stocking conditions, and economic context rather than on a single universal feed formula. Therefore, the present study on the effects of different feeding regimes on mud crab growth performance is important for clarifying which feeding modes most effectively improve growth under culture conditions while maintaining practical relevance for farmers. Its objective is to compare alternative feeding regimes in terms of growth performance and, where applicable, associated production indicators such as survival and feed efficiency, so as to provide evidence that can support more efficient, economical, and sustainable mud crab farming.

2 Growth Characteristics and Nutritional Requirements of Mud Crab

2.1 Growth and molting characteristics of mud crab

Mud crab growth is discontinuous because size increase occurs mainly through molting rather than by steady external enlargement. In juvenile *Scylla serrata*, fresh weight rises abruptly at ecdysis because of rapid water uptake, then increases more moderately during postmolt shell mineralization and tissue deposition, before becoming relatively stable during intermolt (Nguyen et al., 2022). This means that apparent body growth reflects both true tissue accretion and temporary changes in body water, so the molting cycle must be considered when evaluating the effect of feeding regimes on growth performance.

Molting characteristics are shaped by both internal energy allocation and external culture conditions. Juvenile mud crabs consume feed most actively during the first two weeks after ecdysis, and about half of total feed intake during a molt cycle can occur in the first third of that cycle when tissue growth is highest. Environmental factors also modify molt dynamics: in *S. paramamosain*, higher water calcium concentrations shortened molt intervals, accelerated carapace hardening, and increased weight gain during molting, showing that growth responses to feeding depend partly on whether the culture environment supports successful shell formation (Zhang et al., 2024).

2.2 Major nutritional requirements of mud crab

Protein is the dominant dietary requirement for mud crab growth because it supports tissue synthesis, molt-related recovery, and overall biomass gain. A recent review across cultured crab species indicates that crabs generally require about 35%-50% dietary protein and 5%-10% lipid, together with adequate essential amino acids, cholesterol, phospholipids, and long-chain polyunsaturated fatty acids (Esmacili et al., 2024). For juvenile *Scylla serrata*, graded feeding trials showed that the best growth performance and nutrient turnover occurred near 45% crude protein, with regression analysis estimating an optimum of about 46.9%-47.0% dietary protein for maximum growth and protein deposition.

Lipid quality is also critical because crustaceans depend on dietary sterols and essential fatty acids to support molting, development, and survival. Work on *S. serrata* larvae and megalopae emphasized that lipids provide energy as well as cholesterol, phospholipids, and fat-soluble vitamins, and suggested an optimum dietary cholesterol level of about 0.80% for megalopal development in semi-purified diets. Nutrient source additionally matters in practice: soy protein concentrate sustained good tissue growth and feed utilization in juvenile *S. serrata*, indicating that alternative protein ingredients can partially replace fishmeal when diets remain nutritionally balanced.

2.3 Evaluation indicators of growth performance

Growth performance in mud crab feeding studies is usually evaluated with a set of complementary biological and production indicators rather than with body weight alone. Common measures include absolute weight gain, specific growth rate, survival rate, molting percentage, feed conversion ratio, protein retention, and lipid retention, because these variables together reflect whether a diet improves both biomass production and feed-use efficiency. In nursery studies, daily weight gain and specific growth rate in weight are especially useful for distinguishing the effects of different feeds during early development from megalopa to crablet stages (Ly et al., 2024).

The choice of indicator is important because live weight can overestimate real growth during molt-related water uptake, whereas dry matter better reflects actual tissue deposition. Studies on juvenile *S. serrata* therefore recommend evaluating tissue growth on a dry-weight basis, since body water changes markedly across the molt cycle and can obscure nutritional effects on somatic growth. Feed-based indices are equally informative: in purple mud crab instars, commercial formulated feed produced higher survival, greater weight gain, higher specific growth rate, more frequent molting, and lower feed conversion ratio than minced fish, illustrating how multiple indicators together provide a clearer assessment of feeding regime performance (Thien et al., 2022). In summary, mud crab growth performance is best interpreted through the interaction of molting biology, nutrient requirements, and measurement method. For studies comparing feeding regimes, the most reliable evaluation framework combines growth, survival, molting, and feed-utilization indicators while recognizing that true growth is inseparable from the crab's molt cycle.

3 Main Feeding Modes Used in Mud Crab Aquaculture

3.1 Scheduled and quantitative feeding mode

Scheduled and quantitative feeding mode refers to the provision of feed at fixed times and in predetermined amounts relative to crab body weight. In mud crab fattening, this regime is widely used because it standardizes nutrient delivery and simplifies feed management across culture units. Several studies applied fixed feeding rates of 5%-7% body weight per day, usually divided into one or two meals, and reported acceptable growth, feed conversion, and survival under these controlled conditions (Gabito and Baltar, 2023). For example, feeding mud crabs twice daily at 7% body weight supported 100% survival and favorable growth responses when African land snail was used as

feed, indicating that quantitative scheduling can maintain stable production when ration size is matched to animal demand (Figure 1).

Evidence also shows that the optimal quantitative ration depends on production stage and culture system rather than increasing linearly with feed supply. In fattening with raw fish, increasing ration from 4% to 16% significantly improved absolute weight gain and specific growth rate, although survival and FCR did not differ significantly among treatments, suggesting that growth is more sensitive than efficiency to ration adjustment. By contrast, in a recirculating aquaculture system, changing feeding frequency from once to three times daily did not significantly affect growth or survival, although feeding once daily at night produced the best mean growth values, implying that timing can be optimized without necessarily increasing meal frequency (Mayzuri et al., 2025).

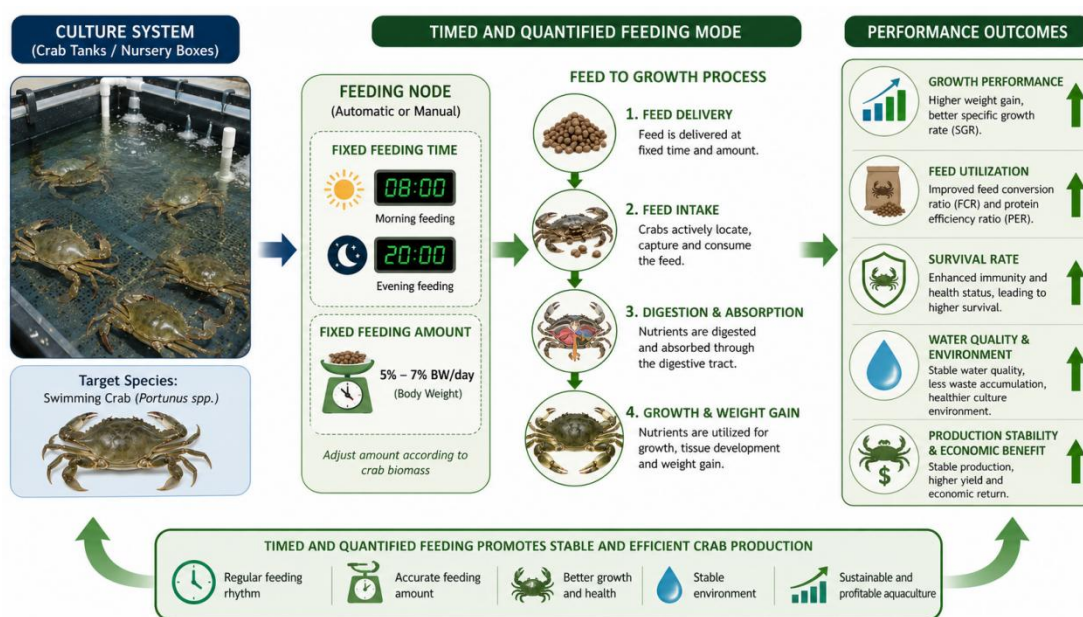


Figure 1 Conceptual framework of scheduled and quantitative feeding management in mud crab aquaculture

3.2 Satiation feeding and restricted feeding modes

Satiation feeding aims to supply feed until intake demand is met, whereas restricted feeding intentionally provides less than that level to improve feed use efficiency or reduce waste. In juvenile *Scylla paramamosain*, reducing ration from optimal to suboptimal and low levels prolonged intermolt duration, increased molting desynchrony, and decreased carapace size and body weight, showing that restriction can directly suppress growth-related processes even when animals still molt successfully (Gong et al., 2022). Starvation was clearly detrimental, because unfed juveniles died without molting, while even low-ration crabs maintained molting success above 95%, indicating that mud crabs tolerate moderate feed limitation better than complete deprivation.

A broader crustacean literature suggests a trade-off between growth maximization under higher feeding allowance and better feed efficiency under restricted rations. In *Penaeus vannamei*, feeding at 80% of apparent satiation improved FCR relative to 100% satiation, but this occurred alongside lower weight gain, demonstrating that restriction can enhance efficiency at the expense of biomass accumulation (Espinoza-Ortega et al., 2026). Similarly, juvenile *Penaeus monodon* showed feed-efficiency benefits under restricted ration and growth benefits from higher feeding frequency, with a significant interaction between frequency and ration size. For mud crab production, these findings support using moderate restriction only when feed cost or water quality control is prioritized over maximum growth.

3.3 Automated and intelligent feeding modes

Automated and intelligent feeding modes extend beyond fixed timers by using behavioral or environmental feedback to decide when to continue, slow, or stop feeding. Conventional automatic feeders generally deliver feed

at preset times and quantities, but such fixed programs can still cause underfeeding or overfeeding because they do not respond to real-time appetite changes (Zhang et al., 2023). This limitation is important for mud crab aquaculture, where feeding demand varies with molt stage, as postmolt juveniles show much higher growth rate and feed conversion efficiency than intermolt individuals.

Recent intelligent aquaculture systems attempt to solve this limitation by combining sensors with machine vision or deep learning. A computer-vision-based feeding system detected wave patterns generated by feeding activity and integrated water-quality sensing, reaching 93.2% accuracy in feeding decisions under aquaculture conditions. Likewise, a dynamic feeding method based on a multi-task neural network achieved 95.44% accuracy in classifying feeding activity while also estimating uneaten pellets, allowing real-time adjustment of feeding intervals and feeding endpoint (Wang et al., 2022). Although these systems were developed mainly for fish rather than mud crabs, they provide a strong technical model for future crab farming because they address the central weakness of fixed quantitative feeding: poor responsiveness to actual feeding demand. Scheduled and quantitative feeding currently has the strongest direct evidence base in mud crab culture, restricted feeding appears to improve efficiency but usually reduces growth, and automated intelligent feeding remains promising but still largely extrapolated from broader aquaculture systems.

4 Effects of Different Feeding Frequencies on Mud Crab Growth Performance

4.1 Weight gain and specific growth rate

Feeding frequency influences weight gain and specific growth rate, but the effect is not uniform across life stage and production system. In grow-out or fattening conditions, several studies found that changing frequency from once to multiple meals per day did not significantly change growth, even when one schedule still produced numerically better results. In a 60-day RAS trial with *Scylla serrata*, feeding frequency did not significantly affect growth or survival, although feeding once daily at 10 pm produced the highest mean weight gain and SGR, reaching 52.00 ± 21.17 g and 5.04 ± 0.14 , respectively (Mayzuri et al., 2025). A second RAS apartment-system study likewise reported no significant effect of feeding once, twice, or three times daily on growth parameters, suggesting that within controlled fattening systems, crabs can maintain similar growth across moderate feeding schedules (Diatin et al., 2026).

Other evidence indicates that more frequent feeding can improve growth when animals are at earlier or physiologically more sensitive stages. In *Scylla olivacea* larvae, feeding rotifers three times daily produced greater absolute growth by day 6 than one or two daily feedings, showing that high-frequency feeding better supports early larval growth. A separate study on mud crabs maintained under different feeding frequencies reported weight growth of 108 g and a daily growth rate of 1.55% with trash fish, indicating that frequency treatment can coincide with measurable growth differences under basket-based maintenance conditions. More broadly, inadequate feed availability suppresses SGR because growth depends on retained energy exceeding maintenance costs, a pattern also observed in juvenile crablets under lower prey availability (Sulaeman et al., 2024).

4.2 Feed utilization efficiency

The effect of feeding frequency on feed utilization efficiency appears weaker and less consistent than its effect on growth. In the RAS apartment-system study, feeding once, twice, or three times daily had no significant effect on feed utilization efficiency or FCR, indicating that increasing meal frequency alone does not guarantee better conversion of feed into biomass (Diatin et al., 2026). This interpretation is consistent with broader nutrition trials showing that mud crab feed efficiency often responds more strongly to diet composition than to feeding schedule. For example, changing carbohydrate and lipid ratios in 35% isoprotein diets did not significantly alter FCR or other feed-efficiency indicators over 60 days (Al., 2024).

At the same time, the wider mud crab literature suggests that efficient feed use depends on matching feeding regime to dietary quality and physiological demand. Juvenile *S. serrata* achieved their best growth and feed efficiency at about 40% crude protein, with improvements in FCR, protein efficiency, and nutrient retention over higher- or lower-protein diets. Feed utilization also shifts strongly across the molt cycle: feed conversion, protein retention,

and energy retention are four to five times higher during postmolt than intermolt stages, showing that the biological timing of intake may be as important as feeding frequency itself (Nguyen et al., 2022). Practical feeding management should therefore consider not only how often crabs are fed, but also whether feed quality and feeding time align with the periods of highest assimilation efficiency.

4.3 Survival rate and molting rate

Survival rate is generally less sensitive to feeding frequency than molting or short-term growth. In the 2025 RAS study, feeding frequency had no significant effect on survival, and the once-daily treatment still achieved 100% survival with a molting rate of 0.67 ± 0.58 . Similarly, the 2026 RAS apartment-system trial found no significant differences in survival rate or molting performance among crabs fed one, two, or three times per day (Diatin et al., 2026). These findings suggest that under controlled fattening conditions with acceptable water quality, moderate changes in frequency alone are unlikely to alter survival substantially.

Molting responses appear more context dependent and can improve with higher feeding frequency when crabs are younger or when nutritional stimulation is stronger. In mud crab larvae, feeding rotifers three times daily increased survival above one- and two-time feeding schedules by day 3 and day 4, indicating that frequent food supply is especially important during early developmental stages. In crablets and instars, better feeding conditions are also linked to higher cumulative molting and improved survival, as shown when higher prey density increased cumulative molting and when a more efficiently utilized formulated diet produced both higher survival and higher moulting frequency than minced fish (Thien et al., 2022). Overall, feeding frequency alone does not consistently drive survival and molting in grow-out mud crabs, but it becomes more influential when combined with vulnerable life stages, limited feed access, or nutritionally superior diets. Across these three outcomes, feeding frequency in mud crab culture appears to have stage-dependent effects: it is often neutral in grow-out RAS systems, but more important for larvae, crablets, and periods of high postmolt nutrient demand.

5 Effects of Different Feeding Times on Mud Crab Growth Performance

5.1 Comparison between daytime and nighttime feeding

The evidence on mud crab feeding regimes centers on day-night timing, feeding frequency, and the link between feeding behavior and culture performance. Across the available studies, outcomes differ by life stage and culture system, so the strongest conclusion is not a single universal schedule but a stage-specific feeding strategy. Mud crabs generally show stronger feeding activity under darkness or during the night at juvenile and grow-out stages, which helps explain why many culture protocols include evening meals. Field observations likewise indicate that *Scylla serrata* remains in its burrow until sunset and then spends the night actively feeding, supporting the view that nocturnal behavior is a core ecological trait in older crabs.

This behavioral pattern can translate into culture performance, although the effect depends on lighting regime and developmental stage. In a recirculating system, once-daily feeding at 10 p.m. produced the best numerical growth, molting, and survival values even though feeding frequency overall was not statistically significant (Mayzuri et al., 2025). However, constant darkness is not uniformly beneficial, because juvenile *S. paramamosain* achieved lower final weight and specific growth rate under 0L:24D than under 12L:12D or 18L:6D, indicating that complete darkness can impair grow-out despite the species' nocturnal tendencies.

5.2 Effects of single feeding versus multiple feeding events

The effect of single versus multiple feeding events is mixed, with larval studies tending to favor more frequent feeding, while juvenile and fattening studies often find little difference in growth across schedules. In *S. olivacea* larvae, feeding rotifers three times daily improved survival on days 3 and 4 and produced greater absolute growth by day 6 than one or two feedings per day (Pattirane et al., 2022). This pattern is biologically plausible because larval feeding strategy is constrained by short gut evacuation and digestion times, making repeated feed delivery more compatible with continuous energy demand during early development.

By contrast, for larger crabs the benefits of more frequent feeding are less consistent. In *S. serrata* reared in RAS, feeding once, twice, or three times daily did not significantly affect growth or survival, and the best numerical performance occurred in the once-daily 10 p.m. treatment (Mayzuri et al., 2025). A separate RAS apartment study also found no significant biological advantage of increasing frequency, although feeding twice daily gave the highest profit and labor efficiency, suggesting that operational optimization may favor moderate frequency even when growth responses are similar (Diatin et al., 2026).

5.3 Relationship between feeding time and feeding behavior

Feeding time is closely tied to mud crab behavior because activity rhythm, prey detection, and digestive physiology shape when feed is most effectively consumed. Juvenile *S. olivacea* respond rapidly to attractive diets, and pellet or natural feed choice appears to be mediated partly by chemosensory cues released into the water, which trigger approach and feeding behavior. Broader evidence also shows that feeding rhythm is related to circadian organization and digestive enzyme activity, so synchronizing feed delivery with active periods can improve feed utilization and reduce waste (Wang et al., 2024).

Importantly, this relationship changes with ontogeny. Zoea of *S. paramamosain* showed a strong diurnal feeding rhythm, with significantly higher feeding rates at 10:00-14:00 from ZI to ZIV, and newly hatched larvae required immediate feeding because they do not retain yolk reserves. In contrast, adult and juvenile field studies show continuous night feeding and only limited daytime feeding, often associated with high tide, indicating a shift from larval daytime peaks to predominantly nocturnal feeding later in life. Overall, the literature indicates that mud crab growth performance is influenced less by a single fixed schedule than by matching feeding time and frequency to developmental stage, behavior, and production system. Night-oriented schedules appear more suitable for juveniles and adults, whereas larvae often benefit from more frequent and partly daytime feeding windows.

6 Effects of Different Feeding Levels on Mud Crab Growth Performance

6.1 Growth rate

Feeding level strongly affects mud crab growth because ration size determines whether enough nutrients remain after maintenance needs are met for tissue accretion and molting (Mayzuri et al., 2025). In a dose-response fattening trial with raw fish, different feeding levels significantly changed absolute weight gain and specific growth rate, showing that ration is not a neutral management variable in *Scylla serrata* culture (Annisa et al., 2024). Evidence from a broader review likewise indicates that trash fish offered at 15% of body weight yields optimal growth and feed efficiency under fattening conditions. At the same time, growth response is not determined by quantity alone, because some studies found that feed formulation differences produced little improvement when protein levels were modest or water conditions fluctuated strongly.

The growth advantage of appropriate feeding also reflects stage-specific metabolic demand. Juvenile *S. serrata* in postmolt stages showed average growth rates of 2.064% initial body weight per day, far above intermolt crabs at 0.492%, while feed intake and nutrient demand for growth were also higher in postmolt animals. This helps explain why stable and appropriately timed feeding tends to improve specific growth rate by maintaining nutrient availability for metabolism and reducing energy loss to stress. Experimental work further shows that once a biologically adequate intake is reached, increasing feeding frequency alone does not necessarily improve growth, since feeding one, two, or three times daily in RAS produced no significant difference in growth parameters, even though one daily feeding gave the best numerical result in that trial (Figure 2) (Diatin et al., 2026).

6.2 Feed conversion efficiency and economic benefits

Feeding level influences production economics primarily through feed conversion ratio (FCR), because lower FCR means less feed is required to produce each unit of crab biomass (Andal et al., 2025). In mud crab polyculture, the treatment with the lower FCR also produced higher absolute growth, reinforcing the general pattern that efficient feed use translates directly into better production output. Evidence from feeding-dose trials is more nuanced, however: one 45-day fattening study found that different ration levels significantly altered growth but did not significantly affect FCR, even though observed FCR values remained relatively high at 1.7-3.8 (Annisa et al., 2024).

This suggests that raising feed input can stimulate growth without always improving conversion efficiency proportionally.

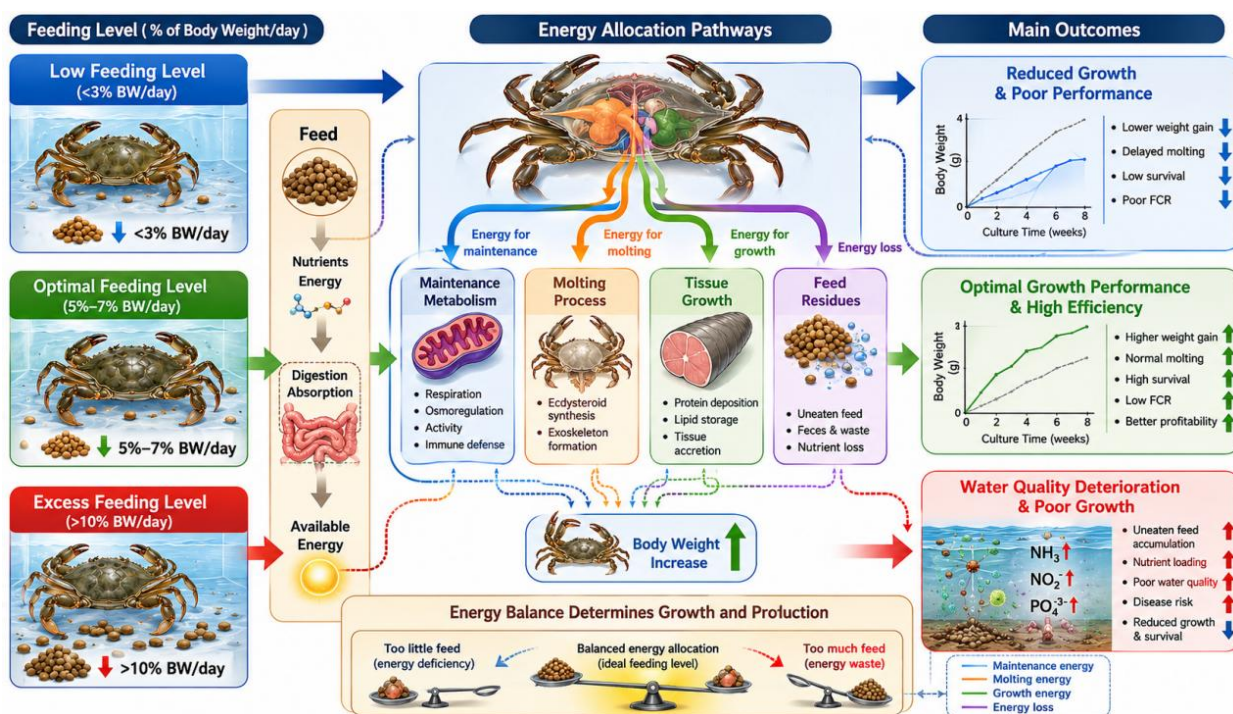


Figure 2 Conceptual model illustrating the effects of feeding level on nutrient allocation, molting activity, and growth performance in mud crab culture

Economic return therefore depends on matching feeding level with feed type and management system rather than simply maximizing ration. In a natural-feed comparison, African land snail produced the best FCR and the highest return on investment, reaching 96.8%, which indicates that biologically efficient feeding can also be financially superior. Another fattening study reported that trash fish achieved the lowest FCR among tested natural feeds and generated a positive ROI of 33.26%, supporting its continued use where supply is reliable (Andal et al., 2025). Operational studies in RAS add that feeding frequency affects labor economics even when biological performance is similar, since feeding twice daily produced the highest profit in one business analysis (Diatin et al., 2026). Feed cost remains the dominant expense in mud crab farming, so inefficient feeding regimes quickly erode margins even when survival is acceptable.

6.3 Risks associated with overfeeding and underfeeding

Both overfeeding and underfeeding impose clear risks on mud crab culture. Underfeeding suppresses growth and molting, while overfeeding promotes feed residue accumulation that can pollute the culture water. The same concern appears in RAS-based work, where inappropriate feeding is linked to slow growth, higher mortality, and declining water quality (Mayzuri et al., 2025). These outcomes are biologically plausible because mud crabs require sufficient digestible energy not only for maintenance but also for molting and tissue recovery; when intake is inadequate, available energy is diverted away from growth.

The practical consequences extend beyond growth depression to broader production instability. Excess residual feed can degrade the rearing environment, and the sustainability literature identifies water-quality deterioration as a recurring constraint that interacts with disease risk and survival across mud crab production systems. By contrast, several feeding studies reported acceptable survival when feeding was paired with water conditions kept within suitable ranges, indicating that feeding risk is partly mediated through environmental management rather than ration alone. Overall, the literature supports a moderate-feeding strategy: enough feed to sustain molting and growth, but not so much that unused feed accumulates, wastes money, and destabilizes culture conditions.

7 Synergistic Effects of Feed Types and Feeding Strategies

7.1 Fresh versus formulated feed

Fresh trash fish remains the dominant feed in mud crab fattening because it is familiar to farmers, protein-rich, and often profitable under short production cycles. Several studies nevertheless identify clear operational weaknesses of this strategy, including unstable supply, seasonality, short shelf life, disease-transfer concerns, and deterioration of water quality when wet feeds are poorly handled (Hadi et al., 2024). In direct fattening comparisons, trash fish also does not consistently produce the best biological response, since alternative fresh feeds such as chicken intestine or African land snail sometimes generated better growth or feed conversion than low-value fish controls.

Formulated feeds, by contrast, are being developed to improve storage stability, handling convenience, and nutritional control, even though their growth advantage over trash fish is still inconsistent. A 30-day fattening trial using dry pellets made from fishery and seafood by-products found that one formulation improved growth response and meat protein content, whereas the trash fish control still achieved better feed and protein efficiency and remained more profitable overall (Senarathna et al., 2021). Other formulation studies similarly reported that artificial diets did not significantly improve growth, molting, or feed efficiency when dietary protein was moderate or when water quality fluctuated strongly, indicating that formulation quality and culture conditions jointly determine whether pellets can replace fresh feeds effectively.

7.2 Mixed feeding and health outcomes

Mixed feeding modes appear promising because they can compensate for the nutritional limits of any single feed source while reducing dependence on trash fish alone. In silvofishery culture of *Scylla olivacea*, combining tilapia with blood clams produced much higher absolute growth and better production than single tilapia feeding, although survival remained similarly high across treatments at 93.33%-96.67% (Wahida et al., 2022). Broodstock evidence points in the same direction: mixed diets combining natural and artificial feeds generally improved spawning output, hatching success, survival, and final body weight relative to either diet alone.

The health value of mixed or diversified feeding lies not only in growth promotion but also in its effects on molting, tissue quality, and system stability. Feed diversification can lower nutritional gaps and reduce overreliance on a single raw material, which is important because mud crab performance depends on feed, rearing system, and environmental management as an integrated package (Diamahesa and Rahmadani, 2024). Related feeding trials also show that improved diet design can raise meat quality or functional performance even when gross growth differences are small, as seen in iso-protein diets where growth was unchanged but meat quality tended to improve in one carbohydrate-lipid ratio, and in formulated feeds supplemented with herbal extracts that increased feed utilization, growth, and molting response (Figure 3).

7.3 Feed quality and strategy matching

Optimizing feeding regimes therefore requires matching feed quality to biological stage, farming objective, and delivery method rather than searching for one universally superior diet. Evidence from formulated-feed studies suggests that mud crabs respond to relatively narrow nutritional windows: feeds around 32%-40% protein and roughly 6%-12% lipid have been associated with favorable growth, while a semi-moist broodstock diet containing 42% protein and 12% lipid produced the strongest somatic and reproductive gains in female mud crabs. At the same time, ingredient quality and physical form matter, because mangrove clam showed strong nutritional suitability as a basal ingredient and high-lipid semi-moist feeds were readily accepted with positive weight gain across treatments (Aaqillah-Amr et al., 2022).

Feeding strategy must also fit ration size, frequency, and pellet stability to the rearing environment. Review evidence indicates that trash fish at about 15% of body weight often gives strong growth and feed efficiency, whereas a raw-fish dosing trial found significant effects of ration level on absolute weight gain and specific growth rate (Annisa et al., 2024). However, feeding frequency in RAS did not significantly alter growth or survival in two recent studies, even though once-daily feeding maximized biological performance in one case and twice-daily feeding gave the best economic return in another, showing that strategy optimization should balance growth, labor, water quality, and

cost rather than weight gain alone (Mayzuri et al., 2025). Across these studies, fresh trash fish remains effective but operationally limited, mixed feeding often improves overall performance, and the best regime is the one that aligns nutrient profile, feed form, ration, and culture system with the specific production goal.



Figure 3 Major feed sources used in mixed feeding strategies for mud crab aquaculture

8 Case Study: Application Effects of Different Feeding Modes in Mud Crab Culture

8.1 Scheduled and quantitative feeding

Scheduled and quantitative feeding in mud crab culture is designed to match ration size and feeding time with the animal's metabolic demand while limiting waste. In fattening systems, this approach often uses fixed percentages of body weight and set feeding times rather than continuously increasing meal frequency. Recent RAS work on *Scylla serrata* found that changing feeding frequency from once to three times daily did not significantly alter survival, growth, molting, or feed utilization, indicating that a stable schedule can maintain performance without requiring more frequent manual feeding (Diatin et al., 2026). Similarly, another RAS experiment reported no significant growth or survival advantage from increasing feeding frequency, and the once-daily treatment still produced 100% survival with 52.00 ± 21.17 g weight gain and $5.04 \pm 0.14\%$ day⁻¹ specific growth rate.

The quantitative component appears especially important when feed allowance, rather than feeding frequency alone, is manipulated. In a crab-box fattening study using raw fish, different feed doses significantly affected absolute weight gain and specific growth rate, while survival and FCR remained statistically similar among treatments,

showing that underfeeding constrains growth more clearly than modest changes in schedule (Annisa et al., 2024). Comparable practical regimes have been used in grow-out studies where mud crabs were fed fixed daily proportions such as 5% or 7% of body weight once or twice daily, and growth outcomes then depended strongly on feed type and efficiency, including FCR values of 1.38 for African snail and 6.90 for trash fish in separate trials.

8.2 High-frequency, small-amount feeding

High-frequency, small-amount feeding is based on the idea that dividing the same daily ration into more meals can improve nutrient capture, reduce competition, and better fit gut evacuation dynamics. This mechanism is particularly plausible in crustaceans because feeding pattern is linked to digestive turnover, and in mud crab larvae, rotifer delivery three times per day improved both survival and growth relative to one or two feedings per day (Pattirane et al., 2022). In *Scylla olivacea* zoeae, the three-times-daily treatment raised survival by 58% on day 3 and by 22% on day 4 over lower-frequency treatments, while also producing higher absolute larval growth by day 6.

Evidence from juvenile and grow-out crustaceans suggests that the benefit of frequent small meals depends on life stage and feeding context. In juvenile *Litopenaeus vannamei*, increasing feeding frequency from three to six and twelve times per day improved final weight, yield, feed conversion, and digestive enzyme activity when the total daily ration was controlled, supporting the physiological rationale for meal splitting (Xu et al., 2020). A factorial study in *Penaeus monodon* likewise showed clear growth benefits of feeding six rather than two times daily, especially when ration size was restricted, suggesting that higher meal frequency can partly compensate for lower per-meal delivery. However, mud crab grow-out results are less uniform than larval data, since RAS fattening studies in *S. serrata* found little or no significant advantage of moving from one or two meals to three meals per day under otherwise stable conditions (Mayzuri et al., 2025).

8.3 Intelligent precision feeding

Intelligent precision feeding extends scheduled feeding by using automation, behavioral feedback, or environmental data to adjust ration and timing in real time. In aquaculture more broadly, intelligent feeding control systems combine models, acoustic tools, or computer vision to determine feeding demand automatically, although current systems still require better accuracy for routine farm deployment. A more integrated precision-feeding framework has also been demonstrated through multi-factor control, where predicted feed requirement is corrected using dissolved oxygen and feeding-activity signals, allowing dynamic adjustment of feed amount instead of relying only on fixed farmer experience (Liu et al., 2023).

Direct mud crab studies on intelligent precision feeding remain limited, but adjacent evidence suggests strong practical relevance for future crab farming. Automatic feeders can improve sustainability by reducing feed waste and enabling feeding schedules to respond to real-time water quality, which is important because overfeeding elevates cost and deteriorates culture conditions (Thornburg, 2025). In intensive shrimp systems, automatic feeding at 6-8 times per day improved body weight, specific growth rate, feed conversion ratio, and profitability relative to manual feeding, indicating that precision delivery can convert the concept of “small, frequent meals” into an operationally feasible strategy. For mud crab, the most defensible conclusion is that intelligent precision feeding is a promising next step, but its value still needs direct validation in species-specific trials that link sensors and automated ration control to molting, survival, and growth performance.

9 Conclusions and Future Perspectives

Different feeding modes affect mud crab growth mainly through feed type, nutrient balance, feeding frequency, and their interaction with culture conditions. Across fattening studies, several natural and wet feeds outperformed conventional low-value fish, but the best option was not identical across experiments because species, size class, culture system, and environmental stability differed. Trash fish performed strongly in some systems and was associated with high growth, efficient feed use, and favorable economic return in fattening. In another trial, trash fish produced the highest weight increment and protein content, with an FCR of 6.90 and positive return on investment. However, African land snail gave the best weight gain, condition factor, feed efficiency, and ROI in a separate grow-out study. Processed chicken intestine also produced better growth and economic performance than

low-value fish, shrimp head waste, and oyster meat in cage fattening, and it gave the best weight gain and molting response among fresh feeds in a single-room system. Formulated diets show promise, but current evidence indicates that formulation quality matters more than formulation alone. Some artificial diet studies found no significant differences in growth, molting, or feed efficiency across tested formulations, suggesting that diets with inadequate protein levels or unstable water conditions can mask treatment effects. Similarly, varying carbohydrate-to-lipid ratios within a 35% isoprotein diet did not significantly affect growth or feed efficiency, although the 31% carbohydrate and 10% lipid treatment showed a favorable trend. More targeted nutrient manipulation appears more effective when aligned with crab physiology: a diet containing 20% starch improved growth and nutrient utilization in juvenile *Scylla paramamosain*, while krill oil supported higher weight gain, specific growth rate, and feed efficiency than linseed oil, with performance similar to fish oil. Feeding frequency appears less influential than feed quality under stable conditions, because RAS culture showed no significant growth differences among once-, twice-, and thrice-daily feeding, although once-daily feeding produced the best overall values. At early life stages, feed choice remains critical, with Lansy pellet feed and frozen *Artemia* producing better growth than pureed shrimp meat and NRD pellets from megalopa to crablet-1.

Precision feeding technologies for mud crab aquaculture are developing toward automated, sensor-linked, and data-driven control of feed delivery. The underlying rationale is strong because feed is a major production cost, and manual feeding often causes waste, labor inefficiency, and inconsistent feeding intensity across ponds. Broader aquaculture research defines precision nutrition as matching dietary composition and feeding strategy to the animal's requirements while minimizing waste. This framework extends beyond simple ration control by integrating genetic background, metabolism, environmental conditions, and production goals. In practical terms, mud crab farming is moving from labor-dependent feeding toward automated and computer-assisted systems, a transition already recognized across aquaculture sectors but still uneven in developing regions. Recent engineering studies show how this transition may occur in crab farming. An IoT-based indoor mud crab system combined automatic feeding with continuous monitoring of pH, salinity, temperature, and water level, and it reported improved growth, reduced mortality, and lower labor demand. Machine-vision monitoring platforms now allow real-time detection of crabs and bait on feeding platforms, with bait detection rates above 90%, offering a basis for adaptive ration adjustment. At the pond scale, RTK-GPS-guided bait casting systems have been designed to achieve variable and spatially uniform feed distribution, with positioning accuracy below 30 cm and continuous feeding speeds up to 240 m² per minute. More advanced feeding boats now incorporate multi-voyage path planning to improve complete bait coverage while reducing repeated paths, turning frequency, and energy consumption. Together, these technologies indicate that precision mud crab feeding will likely combine automated delivery, environmental sensing, machine vision, and algorithmic navigation rather than relying on fixed schedules alone.

Future research should focus on stage-specific feeding strategies, nutritionally optimized formulated diets, and stronger integration between feed management and rearing environment. Current evidence shows that mud crabs do not respond uniformly across life stages or systems. Juvenile and nursery stages appear especially sensitive to feed suitability, salinity, and rearing conditions, with *Artemia*, Lansy pellets, and favorable salinity ranges improving growth or shortening the molting cycle in early-stage *Scylla paramamosain*. By contrast, several grow-out and fattening studies found limited differences among feed treatments when water quality fluctuated or when diets were broadly adequate, indicating that environmental control is often necessary to reveal true nutritional effects. This means future experiments should use better-controlled systems, longer feeding periods, and standardized performance metrics so that dietary effects can be separated from salinity and water-quality noise. Industrial prospects are strongest for feeding systems that reduce dependence on seasonal trash fish while improving feed conversion, labor efficiency, and production consistency. Reviews of mud crab culture already emphasize that sustainable expansion depends on combining suitable feed, rearing system, stocking density, and environmental management rather than optimizing feed in isolation. At the industry level, aquaculture nutrition research points toward more precise requirement estimates, wider ingredient diversification, and greater use of sustainable protein and lipid sources. That direction is directly relevant to mud crab farming, where trash fish remains common but is constrained by seasonality, storage limits, variable quality, and sustainability concerns. Novel ingredient

combinations and processing methods in crab aquaculture more broadly also suggest that performance and product quality can improve together when diets are designed around both biology and sustainability. Overall, the most promising commercial pathway is an integrated model in which balanced formulated feeds, precision delivery systems, and real-time environmental monitoring are deployed together to improve mud crab growth performance reliably and at scale.

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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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Effects of Stocking Density on Yield and Quality of Hard Clams

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Abstract Stocking density is one of the most critical management factors influencing the productivity, profitability, and sustainability of Manila clam (*Ruditapes philippinarum*) aquaculture. Appropriate stocking densities can enhance resource utilization efficiency and maximize yield, whereas excessively high or low densities may adversely affect growth performance, survival, product quality, and environmental conditions. This review summarizes the current understanding of the effects of stocking density on Manila clam culture, with particular emphasis on growth characteristics, biomass production, quality attributes, and environmental impacts. The underlying mechanisms through which density influences food availability, competition, physiological performance, and carrying capacity are discussed. Furthermore, the interactions between stocking density and environmental factors, including water quality, sediment conditions, and disease occurrence, are examined. Recent advances in density optimization strategies, such as stage-specific stocking management, graded culture practices, and precision aquaculture technologies, are also reviewed. Representative case studies from different aquaculture systems are presented to highlight practical approaches for balancing production efficiency and product quality. Finally, future research directions are proposed, focusing on multi-factor interactions, intelligent farming systems, and sustainable aquaculture development. This review provides a comprehensive reference for optimizing stocking density and promoting the sustainable growth of the Manila clam industry.

Keywords Manila clam; Stocking density; Growth performance; Yield; Product quality

1 Introduction

Manila clam, *Ruditapes philippinarum*, is one of the most commercially important cultured bivalves worldwide, contributing about 24%-25% of global mollusc aquaculture production in recent years (Johnson et al., 2025). Its annual global market value has exceeded US\$6 billion, and the species now has a cosmopolitan aquaculture distribution following transfers far beyond its native temperate East Asian range. China remains the leading producer, with production exceeding 2 million tons annually along the Yellow Sea, Bohai Sea, and East China Sea coasts, while Italy is the second-largest producer globally and the dominant producer in Europe. In Italy alone, Manila clam aquaculture generated 23 thousand tons valued at €212 million in 2021, underscoring the species' importance not only to seafood supply but also to regional employment and coastal economies (Martini et al., 2024). At the European scale, clam fisheries and aquaculture have substantial economic value, and production has become strongly dominated by the introduced Manila clam as native clam landings have declined because of overfishing, recruitment failure, abiotic stress, and disease. The expansion of the industry has also been supported by production-system diversification, including integrated culture with shrimp, fish, and crab in China and the extension of farming grounds from intertidal areas into shallow subtidal waters, where longer immersion and higher phytoplankton availability can improve growth opportunities. Beyond direct harvest value, Manila clam farming provides ecosystem services that further strengthen its economic relevance: farm production in Puget Sound has been modeled at 32-45 t per year with additional nutrient credit value exceeding US\$41,000 annually, while life-cycle studies in Italy indicate that clam farming can function as a net carbon sink because shell formation offsets operational emissions. These advantages help explain why Manila clam aquaculture is often regarded as one of the more environmentally favorable forms of animal food production, with relatively low climate impacts and measurable nutrient-removal functions.

Despite that strong economic and environmental profile, Manila clam culture faces mounting production constraints that make husbandry optimization increasingly important. Production has declined in some major farming regions over the past decade, partly because of reduced availability of wild seed, habitat degradation, and climate-related stressors. Climate projections further suggest that habitat suitability for *R. philippinarum* will shift substantially, with decreases in important current producing areas such as parts of the Mediterranean and sections of the Chinese coastline, even as opportunities may open in higher-latitude regions. At the same time, greater reliance on hatchery seed introduces new cost structures and management concerns, because hatchery-based supply can stabilize production continuity but also increase environmental burdens and, if poorly managed, contribute to reduced genetic variability or inbreeding-related performance losses (Wei et al., 2023). Within this context, stocking density emerges as a key aquaculture management factor because it governs how effectively animals convert space, food, oxygen, and husbandry inputs into marketable biomass. Field evidence in juvenile Manila clams cultured in suspended lanterns shows a clear density-dependent decline in shell growth, with larger final shell lengths consistently recorded at lower or intermediate densities than at extra-high densities across batches and sites (Bordignon et al., 2021). Under less favorable water conditions, excessively high density can also sharply reduce survival, showing that density effects are not limited to slower growth but can directly depress final yield through mortality. Comparable patterns appear across other hard-clam and bivalve systems: in *Meretrix lyrata*, high density reduced growth, although intermediate to high density increased tonnage and intermediate density maximized profit; in otter clam, growth was highest at the lowest density, yield rose with density, but economic return peaked at an intermediate level; and in mangrove clam, the highest tested density depressed growth even where survival changed little (Ngô et al., 2025). Hatchery studies reinforce the same principle at earlier life stages: increased larval density commonly reduces shell growth, delays settlement or metamorphosis, and can lower survival or spat yield, even though the exact optimum differs by species and culture stage. Mechanistically, these responses are consistent with stronger competition for food and space, oxygen limitation, and the accumulation of metabolic wastes at high density, whereas very low density can raise production costs and reduce space-use efficiency. Stocking density therefore functions as a classic optimization problem rather than a simple maximization variable: lower densities often improve individual growth and condition, higher densities can raise gross output per area, and intermediate densities frequently produce the best compromise among survival, yield, and economic return.

Against this background, a review focused on the effects of stocking density on the yield and quality of hard clams is timely and necessary. The practical problem for farmers is not merely whether density affects performance, but how density interacts with culture system, seed source, water conditions, predator pressure, and production stage to determine harvest quantity and market quality. Yield is highly sensitive to mortality and seed-related costs in commercial Manila clam operations, and broader hard-clam production analyses show nonlinear relationships between stocking density and farm output rather than a single universal optimum. Density recommendations also vary by context, as seen in soft-shell clam enhancement strategies that favor moderate planting densities under predator protection and in hatchery systems where moderate larval densities improve subsequent spat production. Accordingly, the objective of this review is to synthesize current evidence on how stocking density influences the principal performance traits of hard clams, with emphasis on growth, survival, biomass yield, and quality-related outcomes that determine commercial value. Its scope includes both Manila clam aquaculture, because of its dominant economic role and broad evidence base, and supporting evidence from other hard-clam and clam species where density-dependent mechanisms illuminate general culture principles. Particular attention is given to identifying trade-offs between individual performance and areal productivity, to clarifying why optimal density differs among nursery, grow-out, pond, lantern, and hatchery systems, and to highlighting the implications of density management for sustainability under seed limitation, climate stress, and intensifying aquaculture development. In that sense, the present review frames stocking density not as an isolated husbandry parameter, but as a core lever through which producers can balance biological performance, product quality, environmental conditions, and economic resilience in hard-clam farming.

2 Biological Characteristics and Culture Systems of Manila Clam

2.1 Ecological habits and growth characteristics of manila clam

Manila clam (*Ruditapes philippinarum*) is a dominant intertidal bivalve widely distributed in coastal sediments, especially on tidal flats where exposure at ebb tide and sediment properties strongly shape its habitat use. Its survival and growth depend heavily on benthic behaviors such as burrowing, which improves resistance to currents and predation, and this behavior is affected by substrate particle size, temperature, and salinity (Li et al., 2025).

Growth performance of Manila clam is typically rapid under favorable coastal conditions, helping explain its high fishery and aquaculture value. In Portugal, *R. philippinarum* showed a high growth coefficient, early maturation at about 20.0 mm shell length, and a longer spawning season than the native *R. decussatus*, indicating strong reproductive capacity and fast population turnover (Maia et al., 2025). On the Korean west coast, spat settlement timing and subsequent growth also varied markedly by site, and juveniles settling in autumn at the more favorable site continued growing to adult size by the following May (Kim et al., 2017).

2.2 Major culture systems and their technical features

Current Manila clam farming mainly includes bottom-sowing or on-bottom culture on tidal flats and suspended or caged systems in the water column. Bottom-sowing is widely used because, after seed is released, clams can move, disperse, or aggregate within habitat patches under relatively low direct human interference (Hou et al., 2023). In contrast, suspended systems confine seed in containers or cages and therefore allow tighter control over substrate, depth, and maintenance conditions.

The technical performance of these systems differs in predictable ways. Suspended culture often enhances shell and somatic growth because feeding time is extended compared with intertidal bottom culture, and juvenile clams in subtidal suspended cages grew significantly faster than bottom-cultured controls (Lee et al., 2020). Similarly, suspended containers with deeper substrate improved growth and nutritional condition relative to on-bottom mesh bags, although suspended systems can also experience higher losses if enclosure design allows escape or if fouling is not controlled through regular maintenance.

2.3 Interactions between environmental factors and stocking density

The effects of stocking density cannot be separated from surrounding environmental conditions, because clam performance responds to temperature, salinity, food supply, sediment properties, and oxygen conditions simultaneously. Field evidence shows that adult density can depress individual condition index, while high spat density can reduce recruitment success, indicating that density-dependent competition emerges at different life stages. Sediment grain size, organic carbon, and clam biomass also jointly structure benthic communities in culture areas, showing that density effects propagate through habitat modification as well as direct crowding.

Environmental stress can further amplify density effects by narrowing the range of conditions under which clams maintain growth and survival. Experimental work on other cultured bivalves shows that growth advantages at lower stocking density become especially pronounced at warmer temperatures, with scallops in low-density nets growing 75% faster in summer and performing best within a defined thermal window (Coleman et al., 2021). Likewise, hatchery and larval studies in clams indicate that intermediate or low culture densities generally support better growth and survival when temperature, salinity, food ration, and water exchange are kept within suitable ranges, underscoring that optimal stocking density is always conditional rather than fixed (Guete-Salazar et al., 2025). Manila clam biology and farming strategy are closely linked: the species' rapid growth, sediment-dependent behavior, and flexible culture options make it highly productive, but the outcomes of stocking density depend on how well density is matched to habitat quality, culture method, and environmental stress (Figure 1).

3 Effects of Stocking Density on Growth Performance of Manila Clam

3.1 Growth rate responses under different stocking densities

Across culture stages, Manila clam growth rate generally declines as stocking density increases. In early pre-fattening under controlled upwelling conditions, specific growth rate ranged from 2.3% to 5.0% per day and fell

when density increased, especially when water flow also decreased, showing that density effects emerge even at very small seed sizes (Zanella et al., 2025). A similar pattern was reported for larval culture, where growth decreased significantly as density rose from 5 to 20 larvae·mL⁻¹, and 5-10 larvae·mL⁻¹ was identified as the optimal range for normal larval growth.

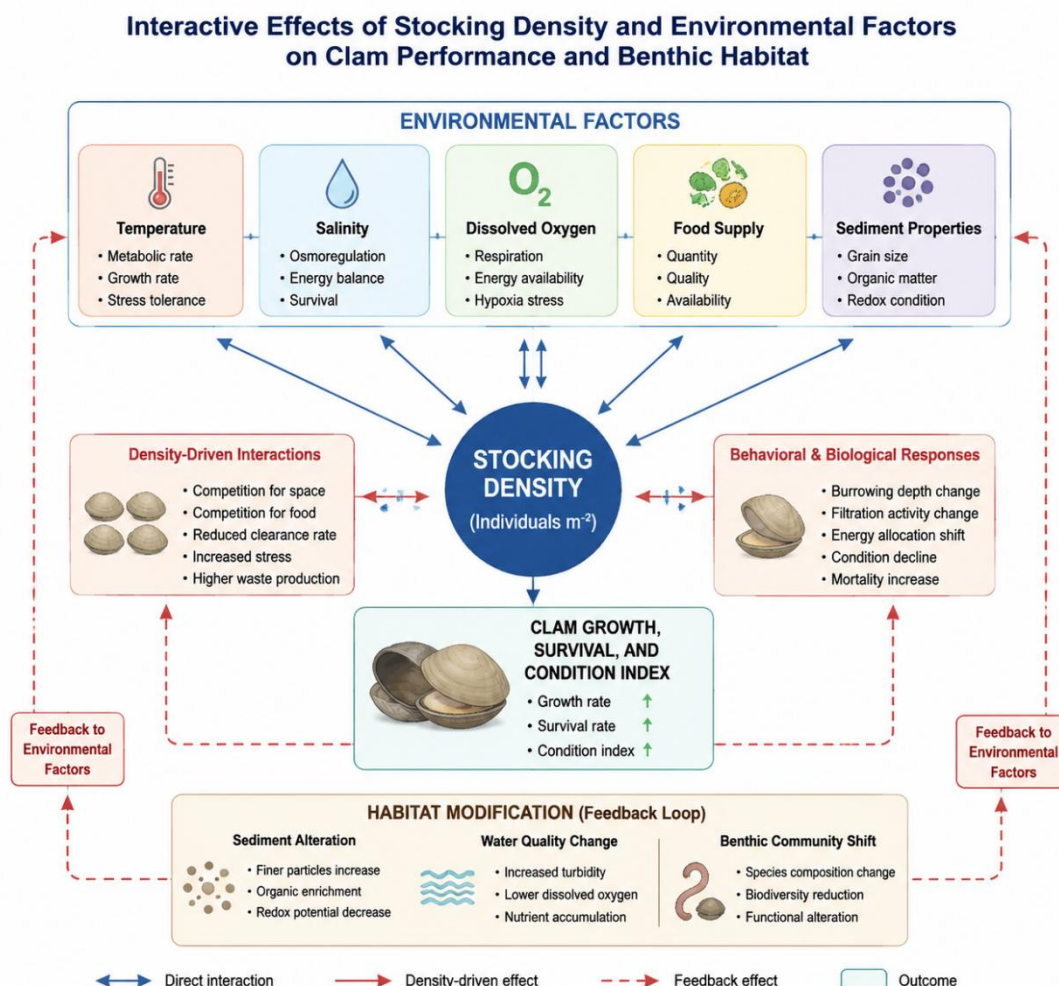


Figure 1 Conceptual framework illustrating the interactive effects of stocking density and environmental factors on clam performance and benthic habitat conditions

The same negative density dependence persists during juvenile and ongrowing phases, although the production optimum is not always the growth optimum. In suspended lantern culture, juvenile shell growth consistently decreased from low or medium densities to the highest density treatments across sites and seed batches, indicating strong crowding effects during pre-fattening (Bordignon et al., 2021). In marine pond ongrowing, the best final size was obtained at 100 clams·m⁻², whereas the highest density tested, 300 clams·m⁻², was considered more suitable for intensive rearing because it better balanced survival and areal yield.

3.2 Effects of density on individual size development

Stocking density has a clear effect on individual size development, particularly shell length, which is one of the most responsive traits to crowding. In suspended lanterns, final shell length decreased stepwise as density increased; for example, B3 juveniles reached 16.1 mm at low density, 14.3 mm at medium density, and 12.7 mm at high density at the western site, with the same overall trend at the northern site (Bordignon et al., 2021). Comparable size depression was also observed in nursery tray culture, where increasing density from 3,019 to 15,094 clams·m⁻² reduced clam growth and condition, indicating that crowding constrains both shell extension and overall individual performance.

Evidence from related clam systems supports the same interpretation and helps explain the mechanism. In Meretrix meretrix larvae, the highest-density treatment produced the smallest mean size at every sampling point, and differences widened with culture time, suggesting that prolonged competition intensifies size divergence. For Manila clam culture in oyster bags, high density reduced growth and altered biometric relationships, with shell height affected more strongly than shell length or thickness, showing that density can influence not only size but also shell form.

3.3 Relationships between stocking density, survival rate, and biomass accumulation

The relationship between stocking density and survival is more conditional than the relationship between density and growth. In Manila clam larval culture, survival was not significantly affected by the tested stocking densities even though growth declined with crowding, indicating that sublethal growth suppression can appear before mortality responses. By contrast, in suspended juvenile pre-fattening, extra-high density sharply reduced survival under the less favorable western-site conditions, with B1 survival dropping to 52.8% versus about 85% at medium and high density, while no density effect on survival was detected at the northern site (Bordignon et al., 2021).

Biomass accumulation therefore reflects a trade-off between individual performance and the number of clams held per unit area. In pond-based intensive culture, 300 clams·m⁻² yielded the highest final biomass, about 4 kg·m⁻², despite not producing the largest individual clams, illustrating why maximum biomass often occurs above the density that maximizes size growth. Field and population studies reinforce this distinction: in Arcachon Bay, relatively low abundance and low somatic production were linked to poor recruitment and moderate growth rather than simple density limitation, while in Korean tidal flats biomass increased over time even as mean density declined, reflecting the contribution of individual growth to standing stock accumulation (Dang et al., 2010). Overall, the evidence shows that increasing stocking density usually reduces Manila clam growth and individual size, while its effects on survival and biomass depend more strongly on site conditions, culture stage, and the balance between crowding losses and areal production.

4 Effects of Stocking Density on Yield Formation in Manila Clam Culture

4.1 Trade-offs between individual productivity and yield per unit area

Stocking density shapes yield formation through a classic trade-off between the performance of each clam and the biomass harvested from a fixed culture area. In Manila clam nursery and juvenile systems, individual growth consistently declines as density rises, as shown by reduced larval growth above 10 larvae·mL⁻¹ and lower specific growth rates in pre-fattening units stocked more heavily (Yan et al., 2006). Yet this decline in individual productivity does not automatically reduce total output, because higher densities can still increase standing biomass per unit area when survival remains acceptable and resource delivery is sufficient.

This distinction between size maximization and yield maximization is especially clear in grow-out studies. In suspended lantern culture, increasing density reduced shell size and the proportion of sowable juveniles, even though moderately high density was still considered operationally useful for pre-fattening (Bordignon et al., 2021). Likewise, demographic modeling projected a maximum Manila clam biomass yield of about 6 kg·m⁻² under optimized seeding and harvest timing, but also showed that strategies maximizing average yield do not necessarily minimize production risk (Figure 2).

4.2 Mechanisms by which density influences resource utilization efficiency

The main mechanism linking stocking density to yield is density-dependent competition for food, space, and water exchange capacity. In early pre-fattening, clam specific growth rate decreased as density increased and water flow decreased, indicating that the biological effect of crowding is amplified when flow-driven food renewal is insufficient (Zanella et al., 2025). A later system comparison similarly found that high-density upwelling and mid-density flat-bottom rearing differed in growth and mortality, and concluded that further gains depend on optimizing density together with water exchange rates (Zanella et al., 2026).

Trade-off Between Stocking Density, Individual Growth, and Total Biomass Yield in Manila Clam Culture

Increasing stocking density reduces individual growth but increases total biomass yield up to a saturation point

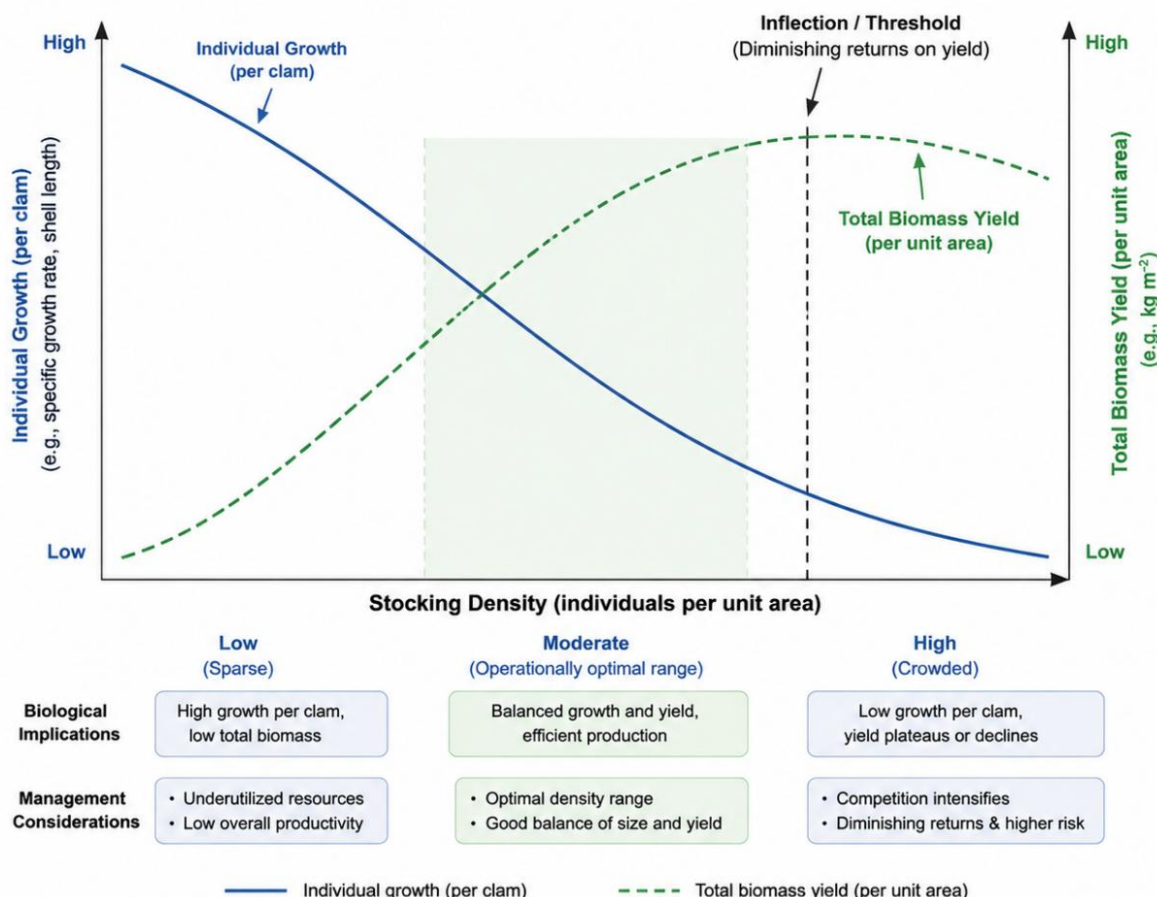


Figure 2 Conceptual trade-off between stocking density, individual growth, and total biomass yield in Manila clam culture systems

At the broader farming scale, excessive density reduces efficiency because stocked biomass can exceed local carrying capacity and convert added seed into mortality rather than harvest. In Jiaozhou Bay, ecological modeling indicated that current Manila clam culture was saturated, and that seeding at $2,500 \text{ ind} \cdot \text{m}^{-2}$ did not significantly improve output but instead increased mortality, reduced individual quality and fatness, and raised production costs (Liu et al., 2021). Long-term field analysis from Tokyo Bay reached a similar management conclusion: introducing juvenile clams beyond the biological productivity of the culture area did not sustain harvestable biomass, so economically feasible production requires matching seeding pressure to expected future stock contribution (Toba et al., 2020).

4.3 Analysis of density thresholds for optimal yield production

The evidence indicates that optimal density is stage-specific rather than universal. For larvae, the best range is low to moderate: $5\text{--}10 \text{ larvae} \cdot \text{mL}^{-1}$ supported normal growth in one hatchery study, whereas another study found that $10\text{--}15 \text{ larvae} \cdot \text{mL}^{-1}$ best balanced growth and survival across $5\text{--}20 \text{ larvae} \cdot \text{mL}^{-1}$. For early pre-fattening in controlled systems, growth remained satisfactory when water flow exceeded about $15 \text{ mL} \cdot \text{min}^{-1} \cdot \text{g}^{-1}$ fresh weight, showing that usable density thresholds depend partly on how much flow is available per unit biomass (Zanella et al., 2025).

For juvenile and grow-out phases, the most productive threshold is generally intermediate rather than extreme. In suspended lantern culture, $30,000 \text{ clams} \cdot \text{m}^{-2}$ was recommended because it maintained good percentages of sowable

clams and lower susceptibility to deteriorating water conditions than 50,000 clams·m⁻² (Bordignon et al., 2021). In open-area culture, carrying-capacity analysis recommended reducing average seeding density to about 700 ind·m⁻² in Jiaozhou Bay (Liu et al., 2021); in Korean cage culture, survival and shell growth both declined as density increased from 100 to 2,000 clams·m⁻², illustrating the sharp penalty of exceeding local tolerance limits. Overall, stocking density influences Manila clam yield not by a simple linear rule, but through a balance between individual growth, survival, and areal biomass. The most defensible conclusion from the available evidence is that moderate, system-specific densities produce the best compromise between marketable size, stable survival, and efficient yield formation.

5 Effects of Stocking Density on Quality Characteristics of Manila Clam

5.1 Condition index and soft tissue development

Stocking density consistently alters soft-tissue development by changing individual growth trajectories and the balance between biomass accumulation and competition for food and space. In suspended pre-fattening systems, increasing density reduced shell length and body weight, with B3 clams at the northern site showing mean weight after 4 weeks of 0.239 g at low density, 0.211 g at medium density, and 0.187 g at high density (Bordignon et al., 2021). A similar density-dependent decline in growth was observed in early pre-fattening upwelling systems, where specific growth rate fell as stocking density increased (Zanella et al., 2025). At the larval stage, growth also decreased significantly with increasing density, and 5-10 larvae·mL⁻¹ supported normal development better than denser treatments. These patterns indicate that excessive crowding suppresses tissue accretion well before market size is reached, thereby lowering the probability of achieving a high condition index at later stages.

Condition index responses appear to depend on both density level and food environment rather than on density alone. On the Korean west coast, the condition index of individual Manila clams decreased as adult population density increased, but increased with higher spat density, suggesting stage-specific density effects. The same study showed that condition index and clam density were affected by chlorophyll *a* in both the water column and sediment, linking tissue condition to food supply under crowded conditions (Kim et al., 2017). Evidence from Arcachon Bay further supports the use of condition index as a sensitive indicator of reproductive and somatic status, while showing that poor population performance can coincide with low gametogenic condition. More broadly, bivalve studies report that condition index and edibility metrics are useful indicators of productive tissue development, even when proximate composition differences between species are limited (Parvathy et al., 2023). Taken together, moderate stocking densities appear more favorable for maintaining soft-tissue fullness and commercial flesh development than either overcrowded or otherwise biologically imbalanced conditions.

5.2 Nutritional composition

Direct evidence on stocking density effects on the proximate composition of Manila clam soft tissue remains limited, but the available literature strongly suggests that density can modify nutritional quality indirectly through growth, energetic status, and food competition. Biochemical assessment methods developed for *Ruditapes* tissues show that protein, lipid, carbohydrate, and nonprotein nitrogen fractions are sensitive indicators of energetic status, and that tissue composition can shift with biological condition, diet, and sex. In Manila clam populations, higher tissue carbohydrate in some organs has been associated with lower relative lipid and protein proportions across physiological states, indicating that nutritional composition is dynamic rather than fixed. Because high density reduces growth in both larval and juvenile Manila clams, it likely changes the partitioning of assimilated energy among maintenance, structural growth, and reserves rather than only reducing size (Yan et al., 2006).

Comparative aquaculture studies reinforce this interpretation by showing that density-related stress can reshape proximate and flavor-relevant composition. In large yellow croaker, medium density improved several muscle-quality traits, while low-, medium-, and high-density groups differed in crude fat, essential amino acids, fatty acids, and aroma-related compounds (Jia et al., 2025). In a multitrophic biofloc system, the highest oyster density reduced the nutritional quality of associated microbial flocs to 14.96% protein and 3.71% lipid, showing that excessive bivalve loading can degrade the nutritional environment of the culture system itself. Baseline bivalve studies also

show broad natural variation in protein, fat, ash, and carbohydrate among clam species and habitats, meaning that any density effect in Manila clam culture will likely interact with locality-specific environmental conditions (Erniati et al., 2023). Thus, density management should be viewed as a nutritional-quality control lever, even though species-specific proximate composition trials for market-size Manila clams are still needed.

5.3 Sensory quality and market value

Evidence directly linking stocking density to the sensory quality of Manila clams is sparse, but the available literature supports a plausible pathway from density to market value through tissue fullness, nutritional condition, and freshness-related attributes. Consumer research on shellfish shows that perceived quality is positively associated with freshness, while attitudes are positively associated with sensory attributes and familiarity. This means that any density regime that weakens flesh development or condition index is likely to reduce commercial appeal even if survival remains acceptable. Since edibility percentage and condition index are commonly used to characterize harvest quality in bivalves, reduced soft-tissue yield under crowding would also be expected to lower unit value in live and processed markets (Parvathy et al., 2023).

Broader aquaculture quality studies suggest that the highest production density is not necessarily the most profitable once eating quality is considered. In fish, medium density can produce superior texture and more balanced flavor profiles, whereas density-related stress at low or high extremes impairs flavor harmony (Jia et al., 2025). A wider welfare review similarly concludes that both excessively low and excessively high stocking densities can damage production outcomes, supporting the idea of an intermediate “golden” density rather than simple maximization of biomass. For clam fisheries and farming systems, stock and biomass levels also shape market supply stability, which is itself an economic dimension of quality; surf clam assessments show that density and biomass vary markedly across habitats and directly affect the capacity to meet market demand. Overall, the literature supports the conclusion that moderate stocking density is most likely to optimize Manila clam sensory quality proxies and market value, although direct taste-panel and postharvest studies in this species remain a clear research gap. In sum, stocking density affects Manila clam quality most clearly through condition index and soft-tissue development, and the broader literature indicates parallel effects on nutritional and sensory quality. The best-supported practical conclusion is that moderate density preserves flesh development and quality better than overcrowding, while the exact optimum remains system- and environment-specific.

6 Effects of Stocking Density on Culture Environment and Health Status

6.1 Impacts of high stocking density on sediment quality

High stocking density can alter sediment conditions by increasing biodeposition and changing benthic biogeochemical processes. In bivalve systems, suspension feeding accelerates the transfer of particulate material from the water column to the bottom, which can increase sedimentation and favor the accumulation of fine organic-rich deposits, especially in shallow or low-energy culture areas (Song et al., 2024). Long-term shellfish farming has also been associated with higher sediment moisture, elevated acid volatile sulfide, and greater concentrations of some heavy metals where hydrodynamic exchange is reduced, indicating that density effects on sediment quality depend strongly on local flushing and farm structure (Ping et al., 2023).

At the same time, sediment effects are not uniformly negative and appear to follow a density threshold. In IMTA mesocosms, benthic clams reduced inorganic nitrogen and phosphate in the water column while modifying sediment microbial communities and increasing the abundance of nitrogen-cycling genes, showing that clam presence can stimulate sediment functions linked to nutrient transformation. For Manila-clam enhancement, benthic fauna and sediment properties were similar to controls and total organic carbon was even lowest in the enhancement area, suggesting that moderate stocking or stock enhancement can have limited sediment impacts compared with more intensive long-term shellfish installations.

6.2 Effects of density variation on water quality and environmental carrying capacity

Density variation has a clear but nonlinear influence on water quality, because moderate clam biomass can improve some indicators whereas excessive biomass can push systems beyond ecological carrying capacity. In integrated

ponds, increasing clam density significantly lowered pH, chlorophyll-a, suspended particulate matter, and total nitrogen, but the overall water-quality index first improved and then declined, with the best performance at an intermediate density rather than the highest one (Yao et al., 2025). A similar pattern appears in blood clam-shrimp polyculture, where doubling clam and shrimp density did not significantly impair water quality, indicating that moderate density increases remain environmentally tolerable when system design and feeding are matched to biological demand (He et al., 2025).

Carrying-capacity studies likewise show that culture performance declines when stocking exceeds available food supply or assimilative capacity. In Jiaozhou Bay, ecological modeling indicated that existing bivalve culture was already saturated, with high mortality rates, and recommended reducing Manila-clam seeding density to about 700 ind.·m² to improve sustainability and culture efficiency. More recent ecosystem-quality modeling estimated shellfish ecological carrying capacity at 33.58 t/km², about 73.3% of the current stocking density, further showing that optimal density is below present practice when ecosystem structure and function are used as evaluation criteria (Song et al., 2025).

6.3 Relationships between density stress and disease risk

High stocking density can increase disease risk indirectly by creating chronic stress, reducing growth, and weakening survival under unfavorable conditions. A broad review of shellfish physiology concluded that chronic stress, especially when combined with microbial, chemical, or abiotic stressors, increases infectious-disease risk, exacerbates morbidity, and reduces recovery potential (Coates and Söderhäll, 2020). In cultured Manila clams, increasing density reduced shell growth consistently and, under less favorable site conditions, sharply increased mortality at the highest density, indicating that density stress lowers resilience when environmental quality deteriorates (Bordignon et al., 2021).

Mechanistically, disease vulnerability under density stress is plausibly mediated through stress-induced disruption of immune processes. Shellfish health assessments increasingly rely on haemocyte counts, enzyme activities, and related biomarkers because stressed individuals may appear externally normal while already showing immunomodulation and reduced immunocompetence. Experimental work on clams further shows that environmental stress can alter metabolic and immune-enzyme responses within hours, and pollutant exposure can suppress hemocyte-based immunity and thereby reduce the capacity to resist external challenges, supporting the view that dense culture becomes most hazardous when it coincides with other environmental stressors (Huang et al., 2025). Overall, stocking density affects hard-clam culture environment and health status through threshold-dependent changes in sediment processes, nonlinear effects on water quality and carrying capacity, and stress-mediated increases in disease susceptibility. The evidence supports managing density below ecological saturation points rather than maximizing biomass per unit area.

7 Density Optimization Techniques and Management Strategies

7.1 Appropriate stocking density allocation at different culture stages

Stocking density should be allocated by culture stage because the biological constraints of larvae, nursery juveniles, and grow-out clams are different. In hatchery culture, excessively high larval density suppresses growth and delays settlement, whereas moderate density provides a better balance between output and seed quality in *Meretrix meretrix*. A similar pattern was reported for *Ruditapes decussatus*, where moderate larval and settlement densities improved survival, growth, and fixation relative to the highest treatments (Azirar et al., 2024). During juvenile and pre-fattening stages, density can be raised above hatchery levels, but only within the carrying capacity of the rearing system. In suspended pre-fattening of Manila clam, 30,000 clams·m⁻² was recommended because it maintained a good proportion of sowable seed while reducing the risk seen at 50,000 clams·m⁻² under less favorable water conditions (Bordignon et al., 2021). For intermediate culture more broadly, lower juvenile densities consistently produced better growth and survival, as shown in raft-cultured razor clams (Figure 3).

At grow-out stage, suitable density should be set not by seed availability alone but by growth-survival-profit tradeoffs. In earth-pond culture of *Meretrix lyrata*, 150 individuals·m⁻² produced the highest economic return, even

though the highest density increased gross productivity (Khôi, 2015). In tidal-zone culture of hard clam *M. meretrix*, growth declined progressively as biomass density increased, and an appropriate range of 249.40-372.38 g·m⁻² was suggested for market-sized animals. Stocking plans should also be adjusted to environmental carrying capacity and season. Ecological modeling from Jiaozhou Bay showed that bivalve stocks had exceeded maximal carrying capacity, and recommended reducing average Manila clam seeding density to about 700 individuals·m⁻² (Liu et al., 2021). The same study found that carrying capacity was lower in summer and autumn because high temperature and filtration demand intensified food limitation.

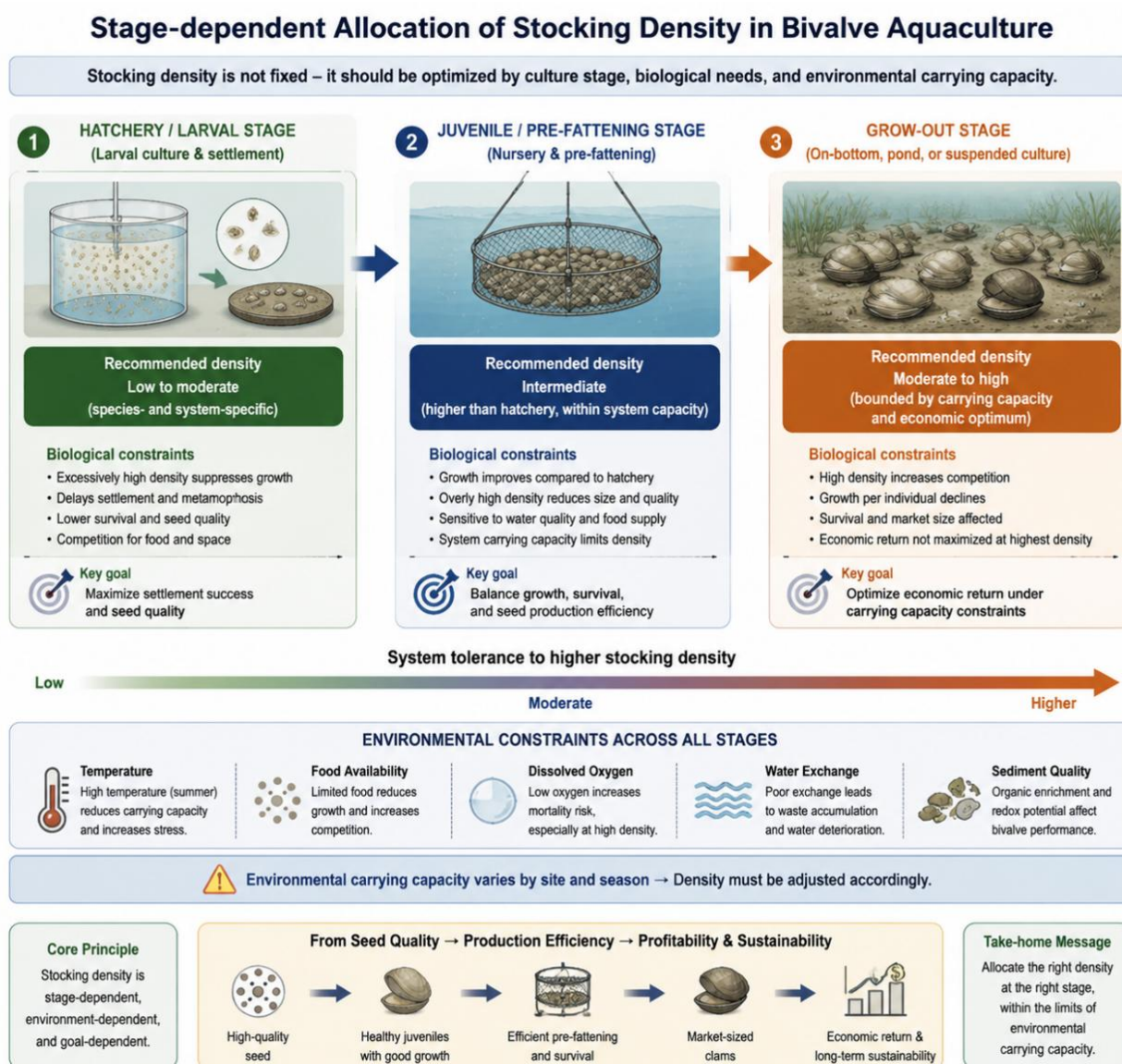


Figure 3 Stage-dependent allocation framework of stocking density across hatchery, juvenile, and grow-out phases in bivalve aquaculture systems

7.2 Graded culture and dynamic density adjustment techniques

Graded culture is justified because the negative effects of crowding strengthen as clams grow and their demand for food and space increases. In suspended mussel culture, density effects became evident only after several months, when animals had reached a larger body size, indicating that higher early density can be tolerated but later thinning is necessary. This principle is consistent with soft-shell clam field culture, where juveniles of 8-10 mm were recommended for spring planting at 333-666 m⁻² so that animals could grow rapidly toward a size refuge. For hard-clam production, graded culture should therefore combine size sorting with timely redistribution of biomass.

Evidence from juvenile Manila clam culture showed that increasing density reduced shell size and the percentage of sowable clams at harvest, even when survival remained acceptable in some treatments (Bordignon et al., 2021). Sediment management can reinforce this strategy, because juvenile Manila clams performed best in poorly sorted sediment with an average grain size of medium sand, which improved survival, growth, and condition relative to less suitable bottoms (Joo et al., 2021).

Dynamic density adjustment should respond not only to size divergence but also to system feedbacks indicating emerging competition. Carrying-capacity analysis showed that oversaturation leads to poor growth and heavy mortality when food and oxygen become limiting, making periodic density reduction a preventive rather than corrective measure. In polyculture systems, clam density also alters plankton structure and ecosystem metabolism, with high-density razor clam treatments depressing macro-, micro-, and nanoplankton biomass and production more strongly than low-density treatments (Zhang et al., 2025). A practical dynamic strategy is to maintain relatively moderate densities at settlement and early nursery phases, then thin or regrade once growth dispersion widens and resource competition intensifies. This approach is supported by evidence that low-density culture improved juvenile performance in both razor clams and soft-shell clams under protected field conditions. It is also compatible with integrated pond systems, where moderate-to-high densities can increase areal yield but excessive crowding reduces individual growth (Ngô et al., 2025).

7.3 Intelligent monitoring and precision aquaculture management

Intelligent monitoring can make density management more precise by detecting when environmental conditions no longer support the standing biomass. Reviews of aquaculture sensing technologies show that IoT-based monitoring of pH, temperature, dissolved oxygen, and related variables improves growth, reduces mortality, and enables rapid detection of abnormal water conditions (Flores-Iwasaki et al., 2025). These parameters are central because water quality is one of the main constraints linking stocking density to performance and product quality in shellfish systems. Real-time monitoring is especially useful for clam culture because density effects often become severe only when oxygen, temperature, or food conditions deteriorate. In suspended Manila clam pre-fattening, the highest density caused marked mortality only under challenging water conditions near harvest, showing that “safe” density is conditional rather than fixed. Continuous monitoring systems are designed for exactly this problem, since they can issue alerts or trigger interventions when dissolved oxygen falls below critical thresholds (Jais et al., 2024).

Precision aquaculture moves beyond observation to automated control. IoT-ML systems have demonstrated continuous tracking of temperature, dissolved oxygen, pH, and turbidity, with thousands of corrective interventions used to maintain survival above 90% in culture ponds (Baena-Navarro et al., 2025). Fuzzy logic control has likewise maintained dissolved oxygen within an optimal range of 6-8 mg·L⁻¹ by dynamically switching aerators in response to real-time sensor input (Nagothu et al., 2024). For hard-clam farming, the management value of these tools lies in linking biomass decisions to live environmental data. Multi-node sensor networks can collect temperature, pH, and salinity data at short intervals with low error, supporting spatially explicit management across ponds or tidal plots. As a result, density adjustment, grading, bottom management, and harvest timing can be based on measured system capacity rather than fixed schedules, which is the most reliable route to stabilizing both yield and quality.

8 Case Studies

8.1 Pond-based culture

Along the Chinese coast, stocking-density optimization in pond-based Manila clam culture has increasingly shifted from empirical seeding toward stage-specific management that matches density to food supply, nursery function, and transfer size. A representative northern China three-phase system combined indoor early spawning, shallow fertilized nursery ponds, and later mudflat grow-out with optimized stocking size and density, shortening the production cycle to about 10-14 months and markedly increasing marketable output. In parallel, ecological carrying-capacity analysis from Jiaozhou Bay showed that production problems under intensive coastal culture were linked to stock saturation, and recommended reducing Manila clam seeding density to about 700 ind.·m² to improve culture quality and efficiency (Liu et al., 2021).

These case studies indicate that pond performance depends not only on absolute density, but also on whether density is synchronized with nursery productivity and subsequent grow-out conditions. Juveniles reared in shallow fertilized nursery ponds grew faster than in the natural environment because of warmer water and richer natural food, showing why relatively intensive early pond phases can support later yield gains when transfer timing is managed well. Yet the Jiaozhou Bay assessment also showed that many existing culture areas had already exceeded carrying capacity and were experiencing high mortality, which means pond intensification without density control can undermine both survival and final harvest stability (Liu et al., 2021).

8.2 Tidal flat systems

In tidal-flat enhancement and bottom-culture systems, density optimization is usually framed as a balance between individual growth, biomass yield, and environmental variability. A demographic model developed from lagoon culture data showed that Manila clam growth and survival are shaped by temperature-driven variation and density-dependent survival, and projected that maximum biomass yield could reach about $6 \text{ kg} \cdot \text{m}^{-2}$ when seeding occurred in spring and harvest in late autumn of the following year (Melià et al., 2004). That same modeling work emphasized a tradeoff between maximizing average yield and minimizing yield variance, which is directly relevant to stocking decisions in enhancement-oriented tidal flats.

Field evidence also shows that the biologically optimal density depends on the production objective. In intensive marine-pond ongrowing, lower density near $100 \text{ ind.} \cdot \text{m}^{-2}$ produced the best final size, but $300 \text{ ind.} \cdot \text{m}^{-2}$ gave the most favorable overall intensive-rearing outcome by combining 84% survival with final biomass of $4 \text{ kg} \cdot \text{m}^{-2}$. Likewise, suspended pre-fattening trials found that increasing density reduced shell size and the proportion of sowable juveniles, while $30,000 \text{ clams/m}^2$ provided a practical compromise between output and robustness under variable water conditions (Bordignon et al., 2021).

8.3 Ecological models

High-efficiency ecological aquaculture models regulate clam density not only to raise harvest output, but also to improve whole-system carbon use, water conditions, and economic performance. In tri-trophic pond polyculture with crab, shrimp, and short-necked clam, the best combined ecological efficiency and economic benefit occurred at $30\text{-}60 \text{ clams/m}^2$, with the intermediate 30 clams/m^2 treatment showing the highest organic-carbon utilization efficiency and the highest shrimp survival and yield. A more recent pond-ecosystem study similarly found that low clam density strengthened the CO_2 sink function through bottom-up stimulation of nutrient cycling and primary production, whereas high density weakened that function through stronger top-down filtering pressure (Li et al., 2024).

Economic and environmental case studies together suggest that moderate density usually outperforms both understocking and overstocking in integrated systems. In Taiwanese hard-clam farms, stocking density had a negative effect on cost efficiency overall, but farms using about $1.1\text{-}1.2 \text{ million clams/ha}$ achieved higher cost efficiency than farms stocked at either lower or higher levels, especially when combined with shrimp or fish polyculture. Evidence from integrated shrimp-bivalve ponds also suggests that a reasonable density increase does not necessarily degrade water quality or phytoplankton structure, indicating that ecological models can sustain higher productivity when density remains within system tolerance rather than exceeding it (He et al., 2025). Across these case studies, stocking density optimization in Manila clam aquaculture is not a single fixed number but a system-specific balance among food supply, survival risk, size targets, and ecological carrying capacity. The strongest recurring pattern is that moderate, stage-matched densities deliver the most reliable gains in yield and quality across pond, tidal-flat, and integrated ecological production systems.

9 Future Research Directions and Development Prospects

Future research on stocking density in hard clam culture should move beyond single-factor experiments and focus on interactive environmental regulation. Recent work on Manila clam pre-fattening shows that growth declines not only as density increases, but also as water flow decreases, indicating that the effect of density depends strongly on hydrodynamic exchange. Similar interaction patterns have been observed in larval clams, where growth, survival,

and ingestion were jointly shaped by stocking density and algal ration rather than by either factor alone. These findings indicate that future density trials should be designed around combined gradients of food supply, flow, and biomass loading so that operational thresholds can be defined more realistically for hatchery, nursery, and field systems. The same multi-factor perspective is increasingly necessary under climate stress and variable rearing conditions. Experiments on clam culture under different hatchery environments show that density effects can shift when temperature, salinity, and water exchange are altered, and that better larval performance is often achieved only when these variables are jointly optimized. Climate-driven studies further show that abrupt salinity decline combined with elevated temperature sharply increases mortality and disrupts feeding, especially in juveniles, which implies that density recommendations based on stable conditions may fail under future coastal scenarios. For this reason, future studies should emphasize density-by-environment models, seasonal risk windows, and life-stage-specific tolerance limits, especially for regions where habitat suitability is projected to decline substantially.

A second major development prospect is the use of smart aquaculture technologies to convert density management from periodic manual adjustment to continuous data-driven control. Precision-aquaculture research shows that modern farms increasingly rely on interconnected sensors, cloud platforms, and predictive analytics to monitor environmental change in real time and support operational decisions. Broader reviews of smart aquaculture similarly indicate that machine learning is already being applied to tasks such as growth estimation, grading, disease detection, and water-quality prediction, providing a technical basis for adaptive stocking decisions. In clam farming, these tools could be used to link standing biomass to dynamic measurements of temperature, salinity, oxygen, and food conditions, thereby allowing earlier intervention before crowding depresses growth or survival. However, digital density management will depend not only on algorithm development, but also on solving practical infrastructure constraints. Research on intelligent aquaculture systems shows that reliable online sensing, low-power transmission, and robust networking remain major bottlenecks, especially in harsh aquatic environments where sensor fouling and communication instability reduce data quality. At the same time, operational studies demonstrate that IoT-AI systems can already support real-time monitoring, predictive control, and remote equipment management with high predictive performance, including growth or production forecasts with R^2 values around 0.94. The next step for Manila clam aquaculture is therefore to build digital twins or surrogate models that integrate biomass density, seed size, flow conditions, and water quality into farm-level decision systems rather than treating stocking density as a fixed preset.

Future high-efficiency Manila clam farming will likely combine density optimization, controlled seed production, and environmental accounting across the full production chain. Recent sustainability assessments confirm that Manila clam farming generally performs well environmentally and can even function as a net carbon sink, while still showing clear hotspots in hatchery electricity use, depuration, and fuel consumption during grow-out. This suggests that future density strategies should not aim only to maximize biomass per unit area, but also to minimize energy-intensive losses and improve survival efficiency across nursery and fattening phases. In parallel, the decline of wild seed supply has made hatchery-based systems increasingly important, even though they can raise environmental burdens unless energy sources and seed-production technologies are improved. Another clear trend is the shift toward larger, better-conditioned juveniles and more resilient farming models. Controlled nursery approaches can stabilize seed supply, reduce early mortality, and produce juveniles that are better able to resist predators and environmental stress after transfer. This will become more important as climate change and biological pressures intensify, since projections indicate major reductions in habitat suitability for Manila clam in parts of the Mediterranean, especially around Italy. Sustainable high-efficiency farming will therefore depend on integrating moderate and stage-specific density control with resilient seed systems, low-impact energy use, and ecosystem-service goals such as nutrient removal and carbon sequestration. Future progress in hard clam density research will depend on treating stocking density as a dynamic system variable shaped by environment, technology, and sustainability targets rather than as a single static culture parameter.

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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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Effects of Salinity Variation on Growth and Health of Yellowfin Seabream (*Acanthopagrus latus*)

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Abstract Salinity is one of the most important environmental factors affecting the growth, physiological regulation, and health status of marine fish. Yellowfin seabream (*Acanthopagrus latus*) is an economically valuable aquaculture species with strong environmental adaptability; however, fluctuations in seawater salinity caused by climate change and intensive aquaculture practices may negatively affect its production performance. This review summarizes the effects of salinity variation on the growth performance, physiological responses, immune function, and molecular regulatory mechanisms of yellowfin seabream. Changes in salinity influence feeding activity, nutrient utilization, energy allocation, osmotic regulation, antioxidant capacity, and disease resistance through complex physiological and biochemical pathways. Salinity stress can induce oxidative damage, alter hematological parameters, and regulate the expression of osmoregulatory and stress-related genes, including ion transporters and antioxidant-related factors. Case studies under different salinity conditions further demonstrate the importance of maintaining suitable salinity ranges for improving growth efficiency and aquaculture sustainability. Future research integrating multi-omics approaches, environmental monitoring technologies, and selective breeding strategies will provide new insights into salinity adaptation mechanisms and promote climate-resilient aquaculture of yellowfin seabream.

Keywords Yellowfin seabream; Salinity variation; Growth performance; Osmoregulation; Aquaculture health management

1 Introduction

Yellowfin seabream (*Acanthopagrus latus*) is a euryhaline sparid widely distributed in the Indo-West Pacific and is recognized as an economically important coastal fish in several Asian production regions. In the northern South China Sea, it has been described as the most economically important sparid species, highlighting its commercial relevance to regional fisheries and aquaculture. The species is also important in the Pearl River Estuary and adjacent traditional fishing grounds, where its value is tied to both capture fisheries and habitat-linked population dynamics (Tang et al., 2023). Its culture potential is strengthened by strong environmental plasticity, because *A. latus* tolerates broad changes in salinity and temperature and can be reared in ponds or cages (Zhao et al., 2025). This euryhalinity is not only commercially useful but biologically distinctive, since the species naturally occupies coastal environments with large and frequent salinity fluctuations and therefore serves as a suitable model for studying teleost osmoregulation. Field evidence further shows that *A. latus* uses habitats spanning low- to moderate-salinity estuarine waters and more marine environments across its life cycle, with repeated migration between these habitats common in many individuals. This ecological pattern helps explain why salinity is a central variable in yellowfin seabream production: hatchery, nursery, pond, and cage systems often expose fish to abrupt or seasonal changes caused by rainfall, freshwater inflow, evaporation, and estuarine mixing. For aquaculture, salinity is therefore not simply a background water-quality parameter; it is a production factor that shapes growth rate, feed use, survival, physiological stability, and ultimately economic return (Seale et al., 2024).

Salinity variation affects fish physiological ecology because osmotic imbalance alters ion and water homeostasis and forces reallocation of energy toward osmoregulation and stress defense (Mkulo et al., 2025). In teleosts, this regulation depends mainly on coordinated responses of the gill, intestine, kidney, and associated epithelial transport systems, which sense environmental change and switch between salt uptake and salt secretion strategies. Across

fishes, growth often improves at intermediate salinities because osmotic costs can be reduced under near-isosmotic conditions, whereas unfavorable salinity increases metabolic demand and suppresses performance. In juvenile yellowfin seabream specifically, a 56-day trial showed that increasing salinity from 6 to 12‰ improved growth, but salinity above 24‰ suppressed growth, indicating that tolerance does not imply equal performance across all salinity levels. Other studies on *A. latus* show that acute salinity challenge causes rapid but partly reversible endocrine and metabolic disturbance: glucose and lactate rise shortly after transfer, cortisol responds at both low and high salinity, and juveniles can acclimate to 5-35 ppt within 48 h under experimental conditions. Gill tissue appears especially important in this adjustment, being highly sensitive under hypoosmotic stress and increasing Na^+/K^+ -ATPase activity to limit ion loss, while the liver shows pronounced oxidative stress responses (Lin et al., 2020). Intestinal responses are also substantial: hypoosmotic exposure reshapes microbial composition, suppresses intestinal Na^+/K^+ -ATPase activity in freshwater, challenges antioxidant defense, and shifts the balance from probiotic taxa in brackish water toward potentially pathogenic bacteria under stronger dilution stress. Salinity-driven microbiota remodeling is not unique to this species, as comparable work in yellow drum found that high salinity altered intestinal microbiota and increased potentially harmful *Vibrio*, reinforcing the idea that fish health under salinity stress includes microbial as well as host physiological dimensions. More recent work in juvenile yellowfin seabream likewise indicates that 10 ppt and 30 ppt conditions produce contrasting gut microbial and transcriptomic states, with brackish water enriching *Cetobacterium* and seawater enriching *Vibrio* alongside different metabolic and immune gene-expression profiles.

Against this background, research on salinity adaptation in yellowfin seabream is significant for both mechanism and application. From a mechanistic perspective, the species is an excellent model because its genome and comparative genomics resources now provide direct entry points into the molecular basis of euryhalinity, including expansion of osmoregulation-related gene families such as *ARRDC3* and *GSTA* and chromosomal resources for studying adaptation across Sparidae. More broadly, omics studies in teleosts show that salinity acclimation involves interacting ion-transport, stress-response, metabolic, and microbiome pathways rather than a single osmoregulatory axis. This systems view is consistent with emerging evidence in *A. latus*: saline-alkaline exposure alters gill histology, increases malondialdehyde, and co-enriches immune- and energy-metabolism pathways even when growth is not significantly changed, suggesting that performance alone can miss substantial sublethal stress. It is also consistent with population-level evidence that salinity-associated SNPs in wild yellowfin seabream are enriched in pathways linked to cellular process, metabolism, immune response, and environmental information processing, implying that adaptation operates through integrated regulatory networks shaped by local environments. For production, this line of research supports species- and stage-specific salinity management rather than assuming that a euryhaline fish performs equally well across its tolerance range. It also supports using salinity as a deliberate management variable to optimize growth, robustness, and disease resistance, while accounting for rate of transfer, developmental stage, and interacting factors such as temperature. Therefore, studying the effects of salinity variation on growth and health of yellowfin seabream is important not only for defining optimal culture conditions, but also for clarifying how physiological regulation, immunity, oxidative balance, and host-microbiota interactions together determine resilience in a fluctuating aquaculture environment.

2 Ecological Characteristics and Salinity Adaptation Basis of Yellowfin Seabream

2.1 Life history characteristics and environmental requirements of yellowfin seabream

Yellowfin seabream (*Acanthopagrus latus*) is a euryhaline sparid widely distributed in the Indo-West Pacific and is an economically important coastal fish in Asian waters (Lu et al., 2022). Its ecological value is closely tied to its broad habitat use, because this species occupies environments where salinity fluctuates frequently and strongly over time. In the Pearl River Estuary, otolith evidence indicates that early life stages are associated with low- to medium-salinity habitats such as mangrove and oyster-farm waters, which likely function as spawning or nursery grounds. Many individuals later move repeatedly between estuarine and marine environments, showing marked habitat plasticity across ontogeny (Tang et al., 2023). This repeated use of habitats with contrasting salinity regimes helps explain why yellowfin seabream is considered a suitable model for studying environmental adaptation in coastal teleosts.

The environmental requirements of yellowfin seabream are shaped not only by its broad tolerance range but also by life stage and the rate of environmental change. In fish generally, the ability to cope with salinity depends on developmental stage, and salinity tolerance often increases markedly from larval to juvenile phases as gill, kidney, and intestinal osmoregulatory functions mature. For yellowfin seabream specifically, experimental evidence shows that juveniles can tolerate wide salinity exposure, but tolerance is strongly modified by temperature and transfer regime. Fish held at 33‰ tolerated salinity as high as 66‰-67‰ when salinity increased gradually, whereas tolerance was lower under more abrupt challenge conditions. These patterns indicate that habitat suitability for this species depends on the interaction of salinity level, temperature, developmental stage, and the speed of salinity fluctuation rather than on a single fixed optimum.

2.2 Physiological regulation mechanisms of salinity adaptation in fish

Salinity adaptation in fish depends on the maintenance of internal osmotic and ionic homeostasis through coordinated regulation of the gill, kidney, intestine, and other epithelial surfaces. Euryhaline fishes are distinguished by their ability to shift dynamically between salt absorption and salt secretion strategies as external salinity changes. This adjustment begins with osmosensing and signal transduction, which detect the direction and magnitude of osmotic disturbance and activate transport and permeability effectors in osmoregulatory tissues. Because these processes consume energy and alter cellular conditions, salinity stress often affects much more than ion balance alone, extending into metabolism, tissue structure, and whole-animal performance. Salinity therefore acts as both an ecological factor and a physiological stressor in cultured fish.

The physiological response to salinity challenge is also mediated by endocrine, cellular-stress, and immune pathways. Hormones such as cortisol, prolactin, growth hormone, and thyroid hormones are central regulators of osmotic acclimation in teleosts, linking ion regulation with metabolism and growth (AlKatrani, 2022). At the cellular level, salinity stress can trigger conserved stress responses involving macromolecular protection, energy reallocation, and in severe cases apoptosis, showing that tolerance depends on the capacity to stabilize cells as well as fluids (Evans and Kültz, 2020). Recent omics-based work further shows that salinity adaptation includes regulation of ion transport genes, stress-response pathways, and microbiota-associated functions, indicating that osmoregulation should now be understood as a multi-system response rather than a single-organ process. This broader framework is especially relevant for euryhaline aquaculture species exposed to repeated environmental fluctuation (Figure 1).

2.3 Research progress on salinity tolerance of yellowfin seabream

Research on yellowfin seabream has moved from basic tolerance description to integrated evaluation of growth, endocrine regulation, tissue response, and molecular adaptation. A 56-day culture study showed that increasing salinity from 6‰ to 12‰ improved growth in juveniles, whereas salinity above 24‰ suppressed growth, indicating that broad tolerance does not mean equal performance across the full salinity range (Mozanzadeh et al., 2021). Short-term challenge experiments further found that juveniles acclimated to 20 ppt could adjust to 5-35 ppt within 48 h, with transient increases in cortisol, glucose, and lactate early after transfer followed by recovery toward basal levels. Together, these studies suggest that yellowfin seabream is physiologically resilient, but its optimal production salinity is narrower than its absolute survival range.

More recent studies have clarified that salinity tolerance in yellowfin seabream is tissue-specific and involves immune, oxidative, and microbial regulation. Under hypoosmotic stress, the gill showed the strongest osmoregulatory sensitivity through increased Na^+/K^+ -ATPase activity, whereas the liver exhibited the most severe oxidative stress response, demonstrating that different organs bear different parts of the acclimation cost. In the intestine, hypoosmotic exposure reshaped microbial composition and suppressed Na^+/K^+ -ATPase activity in freshwater, while potentially pathogenic genera such as *Vibrio* and *Aeromonas* became more abundant under lower salinity conditions (Lin et al., 2020). At the genomic level, chromosome-scale assemblies and population SNP analyses have also identified osmoregulation-related gene family expansion and salinity-associated adaptive loci, supporting a shift in the field toward multi-omics dissection of salinity adaptation mechanisms in this species.

Overall, current research shows that yellowfin seabream salinity tolerance is best understood as an integrated phenotype linking ecology, growth, endocrine response, immunity, and host-microbiota interactions.

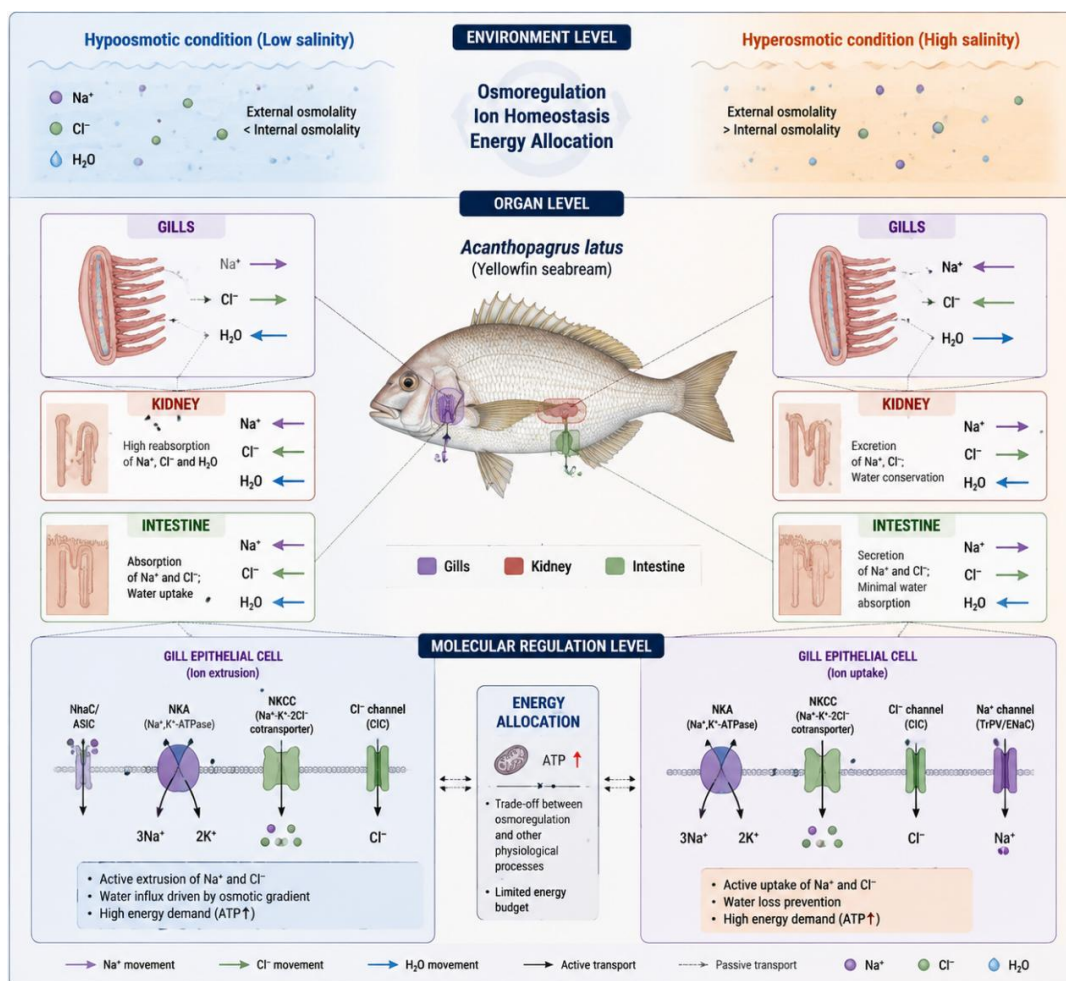


Figure 1 Multi-organ osmoregulatory mechanisms involved in salinity adaptation of euryhaline fish

3 Effects of Seawater Salinity Variation on Growth Performance of Yellowfin Seabream

3.1 Effects of salinity on growth rate and weight gain performance

Salinity variation directly affects growth rate and weight gain in yellowfin seabream, but the response is clearly nonlinear rather than monotonic. In a 56-day trial on juvenile *Acanthopagrus latus*, growth improved when salinity increased from 6‰ to 12‰, whereas further elevation beyond 24‰ suppressed growth, indicating that moderate brackish conditions support better performance than either lower or higher salinity extremes (Mozanzadeh et al., 2021). An earlier acclimation study reached a similar conclusion, showing that juveniles achieved their highest growth at 7 and 15 g/L, while fish transferred to 23 and 30 g/L exhibited poorer performance and even negative growth during the early stage after transfer. These results show that yellowfin seabream can tolerate broad salinity ranges, but its best growth occurs within a narrower intermediate window.

This pattern is consistent with evidence from other euryhaline fishes, where the best growth commonly appears near species-specific isosmotic or low-cost osmoregulatory conditions. In juvenile black sea bream, a closely related sparid, 15 psu was identified as the most favorable salinity for economic culture, with improved feed conversion and low oxidative burden compared with full-strength seawater. Comparable work in Asian seabass also found that intermediate salinity produced the highest weight gain and specific growth rate, whereas both hypo-saline and hyper-saline conditions reduced growth performance (Hassan et al., 2022). Mechanistically, these trends support the view that when salinity departs too far from the physiological optimum, more energy is diverted toward osmoregulation and less remains available for somatic growth.

3.2 Effects of salinity on feeding behavior and feed utilization efficiency

Salinity affects yellowfin seabream growth partly through changes in feeding behavior and feed utilization efficiency. In the same 56-day experiment, salinity above 24‰ not only reduced growth but also impaired feed utilization, showing that performance loss at elevated salinity reflects lower efficiency of converting feed into biomass rather than body weight change alone (Mozanzadeh et al., 2021). Supporting evidence from the 2014 acclimation study showed that the best feed conversion ratio occurred at 7 and 15 g/L, while higher salinity weakened conversion efficiency and coincided with transient weight loss after transfer. This suggests that the feeding response of yellowfin seabream is sensitive to both absolute salinity and acclimation stress.

Evidence from other cultured fishes indicates that salinity can modify feed intake itself as well as post-ingestive efficiency. In Asian seabass, intermediate salinity yielded the lowest feed conversion ratio, while discussion of the same experiment noted that increasing salinity can suppress appetite and thereby contribute to poorer growth. Similar declines in feed intake and protein utilization with rising salinity were reported in common carp and grass carp, where higher salinity increased feed conversion ratio and reduced protein intake, consistent with a shift of dietary energy toward maintenance and ionic regulation rather than tissue deposition. For yellowfin seabream aquaculture, this means that salinity management should be considered part of feeding strategy, because unsuitable salinity can reduce both appetite and feed-use efficiency even when fish remain alive.

3.3 Effects of salinity on body composition and nutrient metabolism

Salinity variation also changes body composition and nutrient allocation in yellowfin seabream. Juvenile *A. latus* reared at 23 and 30 g/L showed reduced proportions of protein, fat, and moisture together with increased ash content relative to lower-salinity groups, indicating that high salinity can alter both tissue deposition and carcass quality. More recent evidence in juvenile yellowfin seabream shows that salinity does not act only at the level of proximate composition, but also reshapes metabolic regulation: fish cultured at 10 ppt upregulated gut-associated metabolic, biosynthetic, and ion-transport genes, whereas fish at 30 ppt showed a stronger immune and redox-oriented transcriptomic profile (Peng et al., 2025). This implies that moderate salinity favors anabolic and nutrient-processing functions, while higher salinity shifts physiological investment toward stress adaptation.

Results from other euryhaline aquaculture species reinforce this interpretation. In GIFT tilapia, increasing salinity decreased whole-body lipid content but increased protein content, demonstrating that salinity can reorganize nutrient partitioning rather than simply depress overall growth. In blue tilapia, brackish-water culture improved growth and was associated with higher amino acid and fatty acid content together with activation of pathways related to unsaturated fatty acid biosynthesis and anabolic metabolism (Zhou et al., 2024). Taken together, these studies suggest that in yellowfin seabream, salinity-mediated differences in growth performance are closely linked to changes in nutrient metabolism, tissue composition, and the balance between anabolic processes and stress-related energy expenditure.

Salinity variation therefore affects yellowfin seabream growth performance through three coupled pathways: direct effects on growth rate and weight gain, indirect effects through feeding and feed conversion, and compositional effects through nutrient metabolism and tissue deposition. For *A. latus*, the evidence consistently indicates that moderate brackish salinity is more favorable than salinity extremes for efficient growth and better physiological allocation.

4 Effects of Seawater Salinity Variation on Physiological Health of Yellowfin Seabream

4.1 Changes in hematological physiological parameters under salinity stress

Salinity stress changes hematological and blood biochemical indices in yellowfin seabream mainly by disturbing osmotic balance and activating a short-term stress response. In juvenile *A. latus*, acute transfer from 20 ppt to 34, 12, or 5 ppt caused significant increases in blood glucose and lactate after 2 h, but both variables returned toward basal levels within 24-48 h, indicating that metabolic disturbance was rapid and largely reversible during acclimation. In the same study, blood electrolytes did not change significantly across salinity treatments, suggesting that juveniles were able to maintain ionic homeostasis even while stress-related metabolites fluctuated. Cortisol and

ALP also rose transiently after transfer and recovered within 24 h, which supports the view that endocrine and biochemical responses are driven more by the timing of challenge than by sustained blood failure.

Although detailed hematology in yellowfin seabream remains limited, studies in related and comparative fishes show a consistent pattern of salinity-induced changes in circulating cells, proteins, and ions. In black sea bream, serum ion concentration and osmotic pressure were actively adjusted within 6-12 h under acute low salinity, showing that blood homeostasis is maintained through rapid regulation rather than passively preserved. In common carp exposed to hypersalinity, total protein, albumin, and globulins decreased while blood glucose, cortisol, and sodium increased, indicating combined osmotic, metabolic, and endocrine strain (Ahmed et al., 2023). A freshwater catfish model showed an even clearer hematological cost, with higher white blood cells but lower red blood cells, hemoglobin, and packed cell volume under salinity exposure, which implies that blood indices are sensitive markers of osmotic challenge severity (Okomoda et al., 2024).

4.2 Effects of salinity variation on antioxidant systems and immune function

Salinity variation strongly affects antioxidant defenses and immune function in yellowfin seabream, but the response depends on tissue and salinity level. Under hypoosmotic stress, the liver showed the most severe oxidative disturbance in *A. latus*, as reflected by fluctuations in SOD and CAT activities together with changes in MDA content. Intestinal physiology was also clearly affected: freshwater exposure significantly inhibited Na^+/K^+ -ATPase activity and challenged the antioxidant defense system, indicating that reduced salinity can impair both ion regulation and redox stability in the gut. At the transcriptional level, hypoosmotic stress altered intestinal expression of genes linked to pathogen recognition, antimicrobial activity, pro-inflammatory cytokines, apoptosis, and antioxidant defense, showing that oxidative and immune responses are tightly coupled in this species.

The immune consequences of salinity stress extend beyond enzyme activity to broader host-microbe and tissue-level regulation. In yellowfin seabream intestine, brackish conditions favored *Lactobacillus* and *Pseudomonas*, whereas freshwater increased potentially pathogenic *Vibrio* and *Aeromonas*, suggesting that low salinity can shift the microbiota toward a less favorable immune context. A newer study likewise found that 30 ppt water enriched *Vibrio* and activated immune and redox-homeostasis genes, while 10 ppt favored *Cetobacterium* and metabolism-related genes, indicating that different salinity regimes bias the fish toward either defense-oriented or metabolic states (Peng et al., 2025). Evidence from black seabream supports the same time-dependent pattern: acute low salinity increased reactive oxygen species, MDA, and total antioxidant capacity early in exposure, then declined as adaptation progressed, showing that oxidative stress is often strongest in the initial adjustment phase (Figure 2).

4.3 Effects of salinity variation on tissue structure and cellular functions

Salinity variation affects tissue structure and cellular function in yellowfin seabream most clearly in organs directly involved in osmoregulation. In *A. latus*, the gill was the most sensitive tissue under hypoosmotic stress and responded by increasing Na^+/K^+ -ATPase activity to reduce Na^+ and K^+ loss, indicating that branchial ion transport is a primary compensatory mechanism. The intestine also showed functional disruption under freshwater exposure, with depressed Na^+/K^+ -ATPase activity and coordinated shifts in microbes, gene expression, and physiological traits, which indicates that salinity stress modifies epithelial function at both cellular and community levels. These findings fit the general teleost model in which gill, intestine, kidney, and other epithelia dynamically switch between salt absorption and salt secretion strategies as salinity changes.

Comparative structural studies show that salinity stress can progress from functional adjustment to overt tissue remodeling when exposure is stronger or more prolonged. In black sea bream, low salinity reduced the number and volume of gill chloride-secreting cells and was accompanied by more developed glomeruli and wider renal tubules, consistent with reduced salt secretion and enhanced ion reabsorption. Across fishes more broadly, salinity challenge can induce gill and liver damage, alter proteins involved in ion transport, metabolism, immunity, and apoptosis, and make gill and intestine the earliest and most responsive organs to structural stress (Su et al., 2025). Acute and chronic salinity experiments in other species similarly show dose- and time-dependent lamellar fusion, intestinal mucosal change, renal stress, and hepatocellular swelling, reinforcing that cellular adaptation has clear structural limits when

salinity moves beyond the optimal acclimation range. Overall, seawater salinity variation affects the physiological health of yellowfin seabream through rapid blood stress responses, tissue-specific oxidative and immune regulation, and remodeling of gill and intestinal function. In yellowfin seabream, physiological resilience is evident, but health costs rise when salinity departs too far from the acclimation range or changes too abruptly.

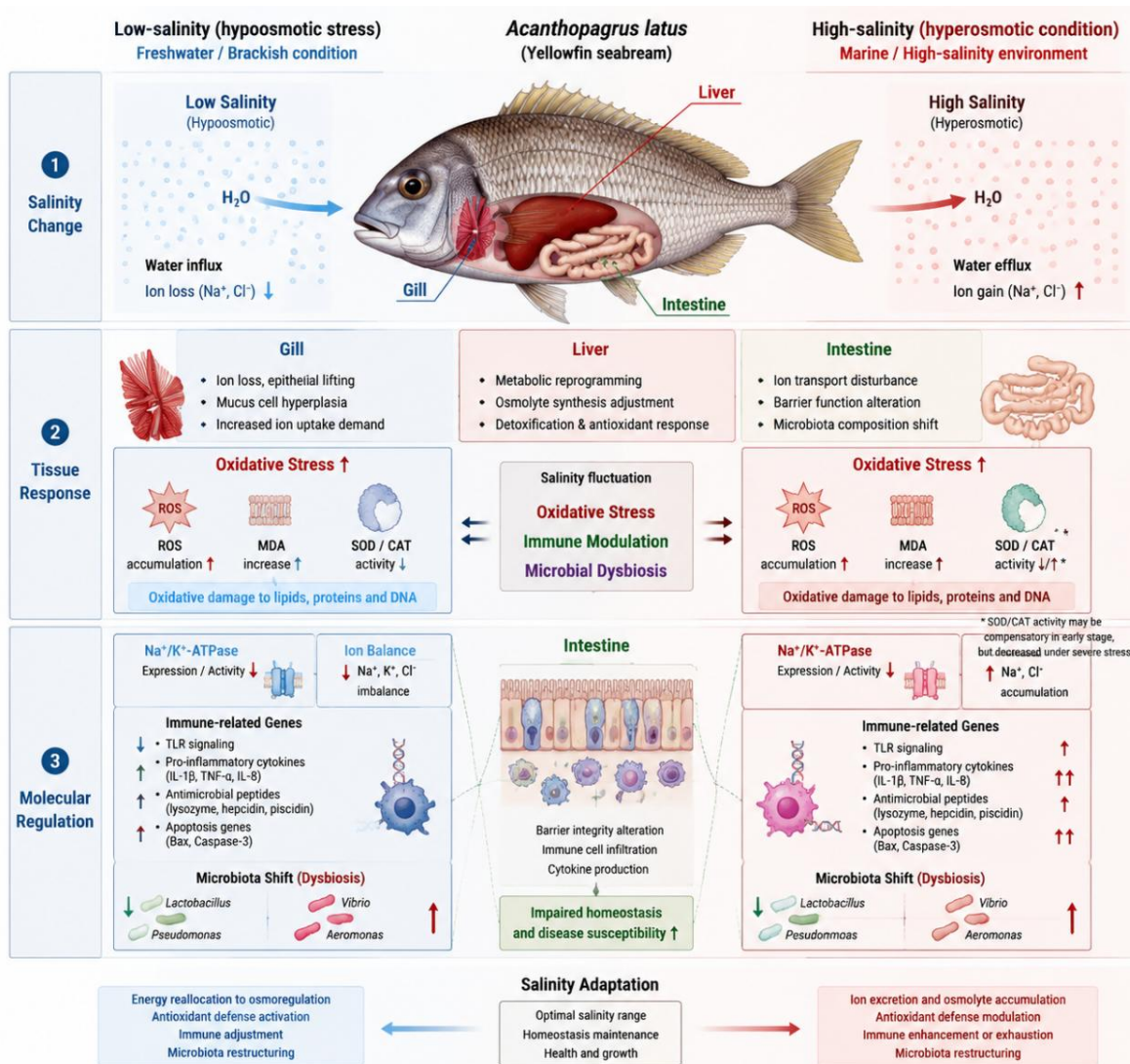


Figure 2 Mechanistic overview of salinity-induced oxidative stress, immune modulation, and microbiota alteration in yellowfin seabream

5 Molecular Regulatory Mechanisms of Salinity-Induced Health Responses in Yellowfin Seabream

5.1 Expression responses of osmoregulation-related genes

In yellowfin seabream, salinity-induced health responses begin with rapid remodeling of osmoregulatory gene expression in key epithelial tissues. Under hypoosmotic challenge, transcriptomic analysis showed that genes related to osmoregulation were strongly altered across gill, liver, and muscle, with the gill being the most sensitive tissue and showing enhanced Na⁺/K⁺-ATPase activity to reduce ion loss. More broadly across euryhaline fishes, salinity acclimation consistently involves ion-transport and water-channel genes, and transcriptomic studies repeatedly identify transporters, osmoregulatory effectors, and stress-response genes as core components of adaptation (Mkulo et al., 2025). This general pattern is directly relevant to *Acanthopagrus latus*, because health maintenance under changing salinity depends on preserving hydromineral balance before secondary oxidative or immune damage develops.

Evidence from related euryhaline fishes helps clarify which genes are likely central to this regulation. In hybrid tilapia gills, salinity stress differentially regulated canonical osmoregulatory genes including CA, AQP1, SLC4A4/NBC1, CLCN2, and SLC12A2/NKCC1, indicating that ion exchange, bicarbonate transport, and water permeability are coordinated at the transcriptional level. In black porgy, another *Acanthopagrus* species, acute salinity transfer increased gill NKA transcripts under both freshwater and seawater challenge, while prolactin receptor expression rose specifically during freshwater adaptation, showing that branchial ion transport is tightly linked to endocrine signaling. Dynamic salinity regimes also appear to rely on especially labile *cfr* and *aqp3* regulation, as shown in tidally reared Mozambique tilapia, suggesting that fluctuating estuarine conditions may favor flexible local transcript control rather than fixed expression states (Seale, 2022).

5.2 Energy metabolism and stress response mechanisms

Salinity adaptation in yellowfin seabream is not only an ion-regulatory process but also an energy-allocation problem, because osmoregulation requires sustained metabolic support. Comparative work in teleosts shows that salinity stress consistently reorganizes metabolites linked to energy production and osmolyte synthesis, indicating that metabolic reprogramming is a basic requirement for osmotic compensation (Mkulo et al., 2025). In yellowfin seabream, hypoosmotic stress caused the liver to experience the strongest oxidative disturbance among examined tissues, with changes in SOD, CAT, and MDA indicating that the metabolic cost of acclimation is closely tied to redox imbalance. This means that salinity-induced health effects are shaped not only by whether fish can regulate ions, but by whether they can supply ATP and limit oxidative damage during that regulation.

Transcriptomic studies in other fishes provide a mechanistic framework for these changes. In spotted sea bass liver, salinity-responsive genes clustered in categories including energy metabolism, ion transport, signal transduction, immune response, and structural reorganization, and the liver was identified as a major source of carbohydrate metabolites for osmoregulatory organs. In spotted seabass exposed to salinity gradients, Na^+/K^+ -ATPase and MDA both rose and then fell over time, while most differentially expressed genes were enriched in energy metabolism, osmoregulation, signal transduction, and immune response, indicating a coordinated time-dependent stress program rather than a single static response (Hu et al., 2024). More detailed multi-omics work in *Pseudobagrus ussuriensis* further showed enrichment of glycolysis, oxidative phosphorylation, HIF-1, TNF, and Jak-STAT pathways under salinity stress, supporting the idea that metabolic reprogramming and stress signaling jointly determine whether acclimation remains adaptive or progresses toward injury (Liu et al., 2025).

5.3 Immune regulation and changes in disease susceptibility

Salinity variation also reshapes immune regulation in yellowfin seabream, and current evidence suggests that this is a central part of its health response rather than a secondary by-product. Under hypoosmotic stress, transcriptomic analysis showed that immune-related differentially expressed genes were widespread across tissues and that T cell-mediated immunity pathways were important in the response of *A. latus*. Intestinal analysis under freshwater exposure likewise revealed differential expression of genes involved in pathogen recognition, antimicrobial function, pro-inflammatory cytokines, apoptosis, and antioxidant defense, indicating that reduced salinity can simultaneously alter barrier defense and inflammatory signaling (Su et al., 2020). These results suggest that salinity stress changes how yellowfin seabream allocates resources between osmoregulation and host defense, which can influence disease vulnerability.

Changes in disease susceptibility are also likely mediated through microbiota and immune trade-offs. In yellowfin seabream intestine, brackish water favored *Lactobacillus* and *Pseudomonas*, whereas freshwater increased potentially pathogenic *Vibrio* and *Aeromonas*, implying that low salinity can shift the microbial environment toward higher infection risk. Comparative studies support this interpretation: in black-chinned tilapia from hypersaline habitats, genes linked to the immune system and heat-shock response were strongly downregulated, suggesting an energetic trade-off between acclimation and immune protection (Blondeau-Bidet et al., 2024). Similar links between low-salinity adaptation, energy metabolism, and disease resistance were observed in *Litopenaeus vannamei*, where the low-salt-tolerant family showed stronger immunity and higher resistance to *Vibrio parahaemolyticus*, supported

by enrichment of energy-metabolism and immune-regulation pathways. Overall, salinity-induced health responses in yellowfin seabream are regulated through three interacting molecular layers: osmoregulatory gene expression, metabolic and oxidative stress control, and immune-microbial regulation. The evidence indicates that health outcomes depend less on salinity tolerance in the narrow survival sense than on how effectively these regulatory systems remain coordinated under fluctuating environmental conditions.

6 Case Studies of Yellowfin Seabream Culture under Different Salinity Conditions

6.1 Case background: effects of salinity gradients on culture performance of yellowfin seabream

Case studies of yellowfin seabream culture under different salinity conditions consistently show that this species is broadly euryhaline, but culture performance varies markedly within that tolerance range. In a 56-day salinity-gradient trial, juveniles reared at 6‰, 12‰, 24‰, 35‰, and 48‰ showed improved growth when salinity increased from 6‰ to 12‰, whereas salinity above 24‰ suppressed growth, indicating that moderate brackish conditions were more favorable than full-strength or hypersaline seawater (Mozanzadeh et al., 2021). A separate acclimation study using 0.5, 3, 7, 15, 23, and 30 g/L reached a similar conclusion, with the highest growth rate and best feed conversion observed at 7 and 15 g/L and poorer performance at 23 and 30 g/L. Together, these studies provide a practical culture background for yellowfin seabream: the species survives over a wide salinity span, but production efficiency peaks within an intermediate salinity window rather than at salinity extremes.

This case background is strengthened by evidence that yellowfin seabream can withstand acute transfer across large salinity ranges, which helps explain its culture potential in estuarine and variable coastal systems. Juveniles transferred from 20 ppt to 34, 12, and 5 ppt acclimated within 48 h, and the main short-term changes were metabolic rather than ionic, showing that salinity stress was rapidly buffered at the whole-animal level. More generally, euryhaline fish maintain homeostasis under changing salinity through coordinated responses of the gill, intestine, and kidney, but rapid shifts beyond the optimal range still cause physiological stress even when survival is maintained (Mkulo et al., 2025). This means that field and farm salinity gradients should be evaluated not only by whether fish remain alive, but by whether salinity stays within the narrower range that supports efficient growth and stable health.

6.2 Case analysis: responses of growth performance and health status

The main growth-response pattern across case studies is that intermediate salinity improves production traits, whereas higher salinity reduces weight gain and feed efficiency. In juvenile yellowfin seabream, growth depression above 24‰ was accompanied by reduced feed utilization, showing that poorer performance at elevated salinity reflects both slower growth and weaker conversion of feed into biomass (Mozanzadeh et al., 2021). Another culture study found that fish reared at 23 and 30 g/L had lower body protein, fat, and moisture together with higher ash content than fish reared at lower salinity, indicating that salinity effects extend beyond growth rate to carcass composition and nutrient deposition. These findings show that salinity gradients shape not only how fast yellowfin seabream grows, but also how efficiently it uses feed and how body tissues are formed during culture.

Health responses in these case studies are similarly salinity-dependent and often precede visible mortality. Acute challenge experiments showed that cortisol, glucose, and lactate rose shortly after transfer and then returned toward basal levels within 24-48 h, indicating a transient but real physiological stress cost during acclimation. Longer-term salinity comparison in juvenile yellowfin seabream further showed that 10 ppt and 30 ppt conditions produced distinct gut microbial and transcriptomic states: brackish water enriched *Cetobacterium* and metabolism-related genes, whereas seawater enriched *Vibrio* and immune/redox pathways (Peng et al., 2025). In case-analysis terms, this suggests that a salinity regime can appear acceptable from a survival perspective while still shifting the fish toward higher immune activation and a less favorable intestinal microbial profile.

6.3 Case implications: optimal salinity regulation and aquaculture management strategies

The main management implication from these case studies is that yellowfin seabream culture should target a moderate brackish salinity range, especially during juvenile grow-out. Across direct growth trials, the best performance clustered around 7-15 g/L or near 12‰, while higher salinity consistently reduced growth or feed

conversion. This pattern aligns with broader aquaculture evidence that the most favorable salinity is often near the point where osmoregulatory costs are minimized and growth can receive a larger share of the energy budget (Mkulo et al., 2025). In practice, salinity regulation for yellowfin seabream should therefore be treated as a production lever rather than only a water-quality constraint.

A second implication is that salinity management should be integrated with acclimation strategy, nutrition, and life stage. Rapid changes caused by rainfall, estuarine mixing, or water exchange can trigger cellular stress responses involving energy reallocation and macromolecular protection, so gradual transfer remains important even in euryhaline species. Nutritional support can also modify tolerance: in black seabream, low-salinity performance improved when dietary cholesterol supported osmoregulation and reduced oxidative and inflammatory stress, while in yellowfin seabream other dietary additives have improved growth and haemato-immunological status under culture conditions. Overall, the case evidence indicates that optimal yellowfin seabream aquaculture depends on keeping salinity within a favorable intermediate range, avoiding abrupt fluctuations, and combining environmental control with nutritional strategies that stabilize health under osmotic challenge.

7 Environmental Regulation Strategies for Yellowfin Seabream Aquaculture under Salinity Variation

7.1 Salinity monitoring and dynamic regulation technologies

Effective salinity regulation in yellowfin seabream aquaculture depends first on continuous monitoring rather than periodic manual measurement. IoT-based pond systems can now track salinity in real time, issue threshold alarms, and support rapid corrective action, which reduces the likelihood that fish experience prolonged osmotic stress (Gulifardo et al., 2025). In automated pond-control trials, fuzzy logic systems maintained salinity within target ranges by activating freshwater pumps as salinity approached upper thresholds, thereby avoiding major deviations that would otherwise stress cultured animals. This type of dynamic control is especially relevant for euryhaline fish raised in estuarine or coastal systems where rainfall, evaporation, and tidal exchange can shift salinity over short time scales (Figure 3).

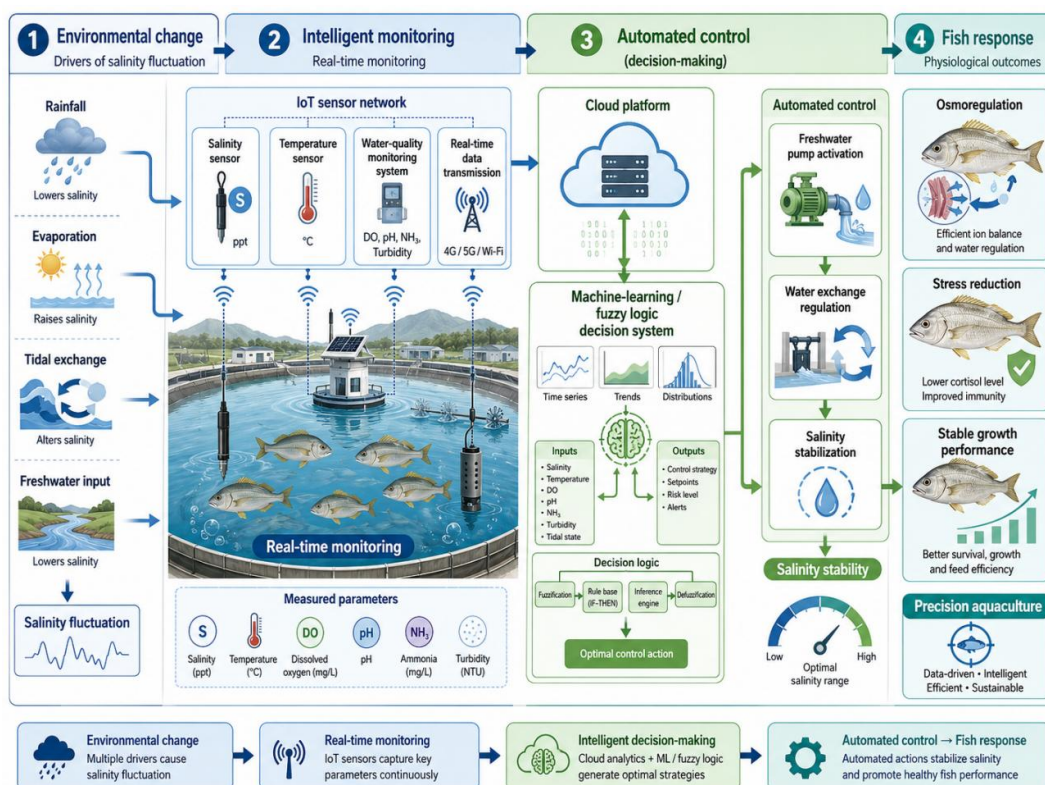


Figure 3 Environmental change-intelligent monitoring-automated control-fish response framework for salinity regulation in yellowfin seabream (*Acanthopagrus latus*) aquaculture systems

Dynamic regulation should also minimize the amplitude and rate of salinity change, because rapid shifts can impose physiological costs even in tolerant species. Machine-learning and sensor-integrated water-quality platforms now allow abnormal trends to be detected early and can automate interventions before water conditions become harmful. Pilot smart-aquaculture systems have shown that digital salinity controllers can stabilize estuarine ponds and accurately track real-time salinity shifts, supporting their use as practical management tools in variable environments (Prasetia et al., 2025). For yellowfin seabream, this means salinity management should aim not only to stay within a safe range, but also to maintain a stable trajectory that avoids repeated acute acclimation events.

7.2 Nutritional enhancement and health management strategies

Nutritional enhancement is a practical way to improve yellowfin seabream resilience when salinity cannot be held perfectly stable. Broad aquaculture evidence shows that dietary interventions can strengthen immunocompetence and stress resistance under environmental challenge, and that nutrient requirements often increase under stressful conditions. Functional nutrition is especially relevant under salinity fluctuation because vitamins, minerals, and amino acids influence mucosal integrity, antioxidant defense, cytokine activity, and immune-cell development, all of which are involved in salinity-linked health outcomes (Kari, 2025). These mechanisms are consistent with yellowfin seabream evidence showing that salinity shifts alter gut microbiota and activate either metabolic or immune-redox pathways depending on the rearing salinity.

More specific dietary strategies from related euryhaline fishes suggest how feeds could be optimized for yellowfin seabream culture. In black seabream, dietary cholesterol under low salinity improved ion reabsorption and osmoregulatory gene expression while reducing oxidative and inflammatory stress, indicating that membrane-related nutrients can directly support acclimation (Bao et al., 2022). In other salinity-stressed fishes, supplements such as myo-inositol and glutamine improved growth, antioxidant capacity, and ion-transport regulation, while selenium nanoparticles enhanced survival and immune performance during low-salinity stress and bacterial challenge. Therefore, health management in yellowfin seabream should combine salinity control with functional feeds targeted at osmoregulation, oxidative balance, and disease resistance rather than relying on environmental adjustment alone (Dildar et al., 2025).

7.3 Ecological aquaculture models and environmental adaptation strategies

Ecological aquaculture strategies under salinity variation should prioritize systems that match the natural adaptive capacity of yellowfin seabream. Because euryhaline species are inherently more suitable for variable-salinity production environments, they provide farmers with greater operational flexibility under climate-driven salinity instability. Recent work in juvenile yellowfin seabream also suggests that brackish-water culture can be advantageous, as 10 ppt conditions favored *Cetobacterium* enrichment and metabolic gene expression, whereas seawater conditions were associated with *Vibrio* enrichment and stronger immune-redox activation (Peng et al., 2025). This supports ecological models that use moderate brackish water as the baseline grow-out environment wherever local hydrology permits.

At the farm scale, environmental adaptation strategies should combine species selection, system diversification, and resilient infrastructure. Reviews of aquaculture under global change argue that cultivating euryhaline or native salinity-tolerant species is a key pathway for maintaining productivity in salinity-affected coastal and inland regions. More generally, farming euryhaline fish has been proposed as a climate-resilience strategy because these species can be reared successfully across different salinities without major loss of basic production capacity (Cusimano et al., 2025). For yellowfin seabream, an ecological aquaculture model should therefore integrate moderate-salinity water sourcing, real-time monitoring, gradual water exchange, and locally adapted production design so that environmental variability is buffered rather than simply endured. In yellowfin seabream aquaculture, the most effective environmental regulation strategy is to link real-time salinity control with targeted nutritional support and brackish-adapted ecological system design. This integrated approach is more consistent with the evidence than treating salinity, feeding, and health management as separate problems.

8 Future Research Directions and Perspectives

8.1 Applications of multi-omics technologies in salinity adaptation research

A key priority is to apply multi-omics technologies directly to yellowfin seabream tissues that mediate osmotic and health responses, especially gill, intestine, liver, and kidney. Recent omics-based reviews show that transcriptomics has already identified core ion transport, osmoregulation, and stress-response genes, while metabolomics has clarified shifts in energy production and osmolyte synthesis during salinity challenge (Mkulo et al., 2025). Multi-omics is especially valuable because it can connect these molecular changes to health-relevant outcomes such as antioxidant disruption, immune activation, and tissue injury, which single-layer datasets often cannot resolve. For yellowfin seabream, the next step is to build species-specific salinity-response atlases across organs, developmental stages, and exposure durations.

Future omics work should also become more granular and predictive. Metabolomics reviews now emphasize the value of LC-MS, GC-MS, NMR, spatial metabolomics, and machine-learning integration for identifying conserved osmotic-response patterns across fish species (Chen et al., 2026). Proteomic and metabolomic studies further show that salinity stress reorganizes pathways related to ion transport, energy synthesis, immunity, apoptosis, and cell-cycle control, especially when stress becomes extreme rather than moderate. Accordingly, future yellowfin seabream studies should move toward time-series multi-omics, single-cell or tissue-resolved profiling, and cross-platform integration with phenotypes such as growth, survival, and gut microbial stability so that biomarkers become usable for both diagnosis and selection (Raza et al., 2025).

8.2 Risk assessment of salinity fluctuations under climate change

Future risk assessment should treat salinity fluctuation as a dynamic climate hazard rather than a static water-quality variable. Climate change is expected to alter aquaculture through sea-level rise, saltwater intrusion, flooding, precipitation shifts, warming, and dissolved oxygen decline, all of which can reshape salinity regimes and fish health simultaneously. Because stress responses depend not only on absolute salinity but also on exposure rate, duration, and interaction with other drivers, yellowfin seabream risk models should explicitly incorporate compound-stressor scenarios instead of evaluating salinity in isolation. This is particularly important in coastal pond and estuarine systems where short-term hydrological events can rapidly move culture water outside optimal ranges.

A second research need is to connect environmental forecasting with biological vulnerability and socioeconomic consequences. Regional studies already show that climate-driven aquatic salinization can reduce habitat suitability and disproportionately affect poor communities that depend on fisheries and aquaculture. However, local outcomes are not uniform: in some transition zones, farmers have responded to changing salinity patterns through water-use shifts and diversification into mixed rice-shrimp-prawn-fish systems, improving production and livelihood security (Bhowmik et al., 2023). For yellowfin seabream aquaculture, future work should therefore combine salinity monitoring, hydrological modeling, early-warning systems, and farm-level adaptation trials to identify where this species can provide climate resilience and where salinity variability will exceed safe production thresholds (Froehlich et al., 2018).

8.3 Selective breeding and genetic improvement for salinity tolerance in yellowfin seabream

Selective breeding for salinity tolerance in yellowfin seabream should be developed as a genetically informed, polygenic program rather than a search for single major genes. Work in tilapia shows that salinity tolerance is a complex trait, but GWAS can still identify useful loci, including missense variants associated with more than twofold longer survival under high-salinity challenge (Huang et al., 2024). Reviews of aquaculture genomics also show that marker-assisted selection is helpful when robust QTL are available, whereas genomic selection is better suited to traits controlled by many loci of small effect. For yellowfin seabream, this means future breeding should combine accurate salinity phenotyping with dense genomic markers and validation across families, life stages, and farming environments.

The most promising long-term strategy is to integrate genome resources, selection models, and functional biology. In salinity-tolerant tilapia, genome improvement, QTL mapping, GWAS, and candidate-gene polymorphism

analysis are viewed as essential steps for accelerating molecular breeding (Yue et al., 2023). New genomic-selection work in spotted sea bass further shows that combining marker types can substantially improve prediction accuracy for tolerance traits, reaching an accuracy of 0.71 in the best-performing integrated model (Zhang et al., 2025). Yellowfin seabream breeding programs should therefore prioritize reference-genome quality, high-throughput salinity challenge phenotyping, and genomic prediction pipelines that can be updated with omics-derived biomarkers of osmoregulation and stress resilience, while also preserving growth and health traits needed for commercial culture. Overall, future research on yellowfin seabream should connect pan-omics biology, climate-resilient risk assessment, and genomic breeding into one framework. That integrated approach is the clearest path to defining optimal salinity management and improving health and productivity under increasingly variable culture conditions.

9 Conclusions

Salinity variation is one of the most important environmental factors influencing the growth performance of yellowfin seabream. As a euryhaline marine fish, this species has a certain capacity to tolerate a relatively wide salinity range, but its growth response is not uniform under all conditions. When salinity remains within an appropriate physiological range, yellowfin seabream can maintain stable feeding activity, efficient nutrient assimilation, and normal metabolic function, thereby supporting satisfactory growth rate and body weight gain. In contrast, exposure to excessively low, high, or rapidly fluctuating salinity often increases the energetic cost of osmoregulation, causing more metabolic resources to be diverted from somatic growth toward physiological adjustment and survival maintenance. Overall, the growth performance of yellowfin seabream tends to depend not only on the absolute salinity level but also on the duration, amplitude, and frequency of salinity change. Moderate and relatively stable salinity conditions are generally more favorable for feed utilization efficiency, protein deposition, and body composition balance, whereas persistent salinity stress can suppress appetite, reduce feed conversion efficiency, and impair normal growth trajectories. Therefore, salinity should be recognized as a central regulator of production performance in yellowfin seabream aquaculture, and growth optimization requires maintaining environmental salinity within a biologically suitable and dynamically manageable range.

Beyond growth, salinity variation has comprehensive effects on the physiological health of yellowfin seabream. Changes in salinity can alter hematological characteristics, ionic balance, endocrine responses, antioxidant capacity, and immune status, reflecting the broad systemic nature of salinity adaptation. Under manageable salinity conditions, yellowfin seabream can activate osmoregulatory and metabolic adjustment mechanisms that help preserve internal homeostasis. However, when salinity stress exceeds the adaptive threshold of the fish, disturbances begin to appear in blood biochemical indicators, oxidative stress regulation, tissue integrity, and cellular function, indicating that health impairment often accompanies environmental instability. The health consequences of salinity stress are also closely linked to the intensity and duration of exposure. Short-term salinity shifts may trigger compensatory responses that are initially protective, but long-term or repeated stress can weaken antioxidant defenses, increase susceptibility to inflammation or infection, and damage key organs such as the gills, liver, kidney, and intestine. At the molecular level, these outcomes are associated with changes in the expression of genes related to ion transport, energy metabolism, stress signaling, and immune regulation. Taken together, the available evidence indicates that salinity variation affects yellowfin seabream health through integrated physiological, biochemical, histological, and molecular pathways, making health assessment essential when evaluating the biological effects of salinity in culture systems.

From an aquaculture perspective, effective salinity management is essential for improving both productivity and animal welfare in yellowfin seabream farming. Maintaining salinity within an appropriate range, avoiding abrupt fluctuations, and adjusting culture conditions according to developmental stage and environmental context can help reduce physiological stress and support stable growth and health outcomes. In practice, salinity regulation should be combined with water quality monitoring, nutritional support, and health management strategies so that fish can better cope with environmental variation. This integrated approach is particularly important in coastal and estuarine farming areas, where rainfall, evaporation, tidal exchange, and freshwater input can cause pronounced salinity

instability. Future applications in yellowfin seabream aquaculture should move beyond simple salinity control toward more precise and adaptive management frameworks. The use of real-time monitoring technologies, automated environmental regulation systems, and data-driven culture models could improve the prediction and mitigation of salinity stress under commercial conditions. At the same time, selective breeding for salinity tolerance, together with molecular and multi-omics research on adaptive mechanisms, may provide new opportunities to develop more resilient stocks. In the context of climate change and increasing environmental variability, advancing salinity management from passive response to proactive regulation will be a key direction for sustainable yellowfin seabream aquaculture.

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Conflict of Interest Disclosure

The authors affirm 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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Characteristics of Water Quality Changes in Cage-Cultured Grouper

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Abstract This study investigates the water quality dynamics in grouper (*Epinephelus* spp.) cage aquaculture systems, with a focus on identifying spatiotemporal variation patterns, driving mechanisms, and their ecological implications. Based on field monitoring and systematic analysis, key water quality parameters-including temperature, salinity, dissolved oxygen, pH, nutrients, and organic matter-were evaluated to characterize environmental variability within and around cage farming areas. The results indicate that water quality exhibits pronounced diurnal, seasonal, and spatial heterogeneity, primarily driven by tidal exchange, hydrodynamic conditions, and meteorological forcing. Aquaculture activities, particularly feed input and metabolic waste release, significantly contribute to nutrient enrichment and organic load accumulation, which may further alter microbial community structure and ecosystem stability. External environmental factors, such as rainfall events, wind-driven mixing, and adjacent coastal pollution inputs, also play important roles in modulating water quality fluctuations. A case study from a representative aquaculture region further demonstrates the interaction between farming intensity and environmental response. Finally, the study discusses the impacts of deteriorating water quality on grouper physiological stress, disease susceptibility, and growth performance, and proposes integrated management strategies including ecological carrying capacity control, real-time monitoring systems, and sustainable aquaculture practices. These findings provide scientific support for optimizing cage aquaculture management and improving coastal water environmental sustainability.

Keywords Grouper aquaculture; Cage culture; Water quality dynamics; Spatiotemporal variation; Environmental management

1 Introduction

Grouper cage aquaculture has expanded rapidly in tropical and subtropical coastal waters and is now a major marine fish farming sector in Asia, supplying high-value protein and income for coastal communities. This growth coincides with broader global expansion of marine cage culture, where waste discharge, nutrient loading, and associated changes in water quality are recognized as key limiting factors for sustainable development (Zhang et al., 2020). Water quality shapes fish physiology, behavior, health, and welfare; changes in temperature, turbidity, dissolved oxygen, salinity, pH, inorganic nitrogen, and emerging pollutants can produce profound effects on metabolism, organs, and behavior that ultimately determine growth and survival in culture systems (Zhang et al., 2024). Against this backdrop, clarifying the characteristics of water quality changes in cage-cultured grouper has both scientific and practical significance for optimizing production, safeguarding fish welfare, and protecting surrounding coastal ecosystems.

Grouper production now involves at least dozens of species and hybrids, with Asia dominating global output and many small-scale farmers depending on this activity for employment and income. Hybrid groupers, such as crosses between tiger grouper (*Epinephelus fuscoguttatus*) and giant grouper (*E. lanceolatus*), have been widely adopted because of high growth potential, production efficiency, and resilience, supporting commercial-scale farming across the Asia-Pacific region. Grouper culture is now recognized as one of the highest-yielding marine aquaculture sectors in China, where hypoxia and other environmental stresses associated with intensified production, elevated temperatures, and high-density transport have become major constraints (Wang et al., 2026). At the same time, eco-friendly aquaculture management technologies are being promoted to increase grouper output per unit area while reducing water and energy use, showing that management innovations can enhance both economic returns and resource efficiency (Cheng et al., 2024).

Despite these advances, water quality dynamics remain a central scientific and management challenge in cage-cultured grouper. Marine cage farms discharge uneaten feed, feces, metabolites, and dissolved nutrients directly into surrounding waters, creating risks of eutrophication, oxygen depletion, and harmful shifts in plankton and microbial communities. Comparative studies between grouper cages and nearby non-aquaculture waters show significantly elevated dissolved inorganic nitrogen and soluble reactive phosphorus near cages, along with altered bacterial communities and strong correlations between microbial taxa and nutrient levels, highlighting eutrophication impacts of cage farming. Multi-parameter analyses in marine aquaculture areas further indicate that temperature, dissolved oxygen, salinity, inorganic nitrogen, chlorophyll a, and even antibiotic resistance genes are key drivers of temporal and spatial water quality variation, with cage systems strongly influenced by aquaculture activities and seasonality (Zhang et al., 2020).

Within cages, suboptimal water quality directly affects grouper physiology and health. For hybrid and cantang groupers, water quality factors such as ammonia and nitrite show strong correlations with cortisol levels, indicating that nitrogenous wastes act as major stressors in floating-net systems (Sulmartiwi et al., 2022). Experimental exposure to sub-lethal and acute concentrations of waterborne ammonia in juvenile hybrid groupers causes hematological disturbances, oxidative stress, altered antioxidant enzyme activities, and pronounced stress responses, including increased plasma cortisol and inflammatory and apoptosis gene expression, underscoring their sensitivity to nitrogen accumulation. Moreover, poor or imbalanced water quality can exacerbate disease outbreaks, as seen in humpback grouper cages where viral nervous necrosis is associated with stress and where temperature, dissolved oxygen, salinity, nitrate, and phosphate are critical parameters for maintaining health and preventing viral replication (Yanuhar et al., 2020).

Although many studies have identified sets of “critical” water quality parameters—typically including pH, dissolved oxygen, turbidity or suspended solids, and various forms of inorganic nitrogen—for cage systems in different regions, there is still no unified, species- and site-specific understanding of how these variables co-vary over time in grouper cages and how these dynamics translate into physiological stress, behavior changes, and production outcomes. Existing work in marine aquaculture areas has applied multivariate methods such as principal component analysis to identify dominant gradients and key drivers among temperature, salinity, dissolved oxygen, nutrients, organic matter, chlorophyll, and antibiotic resistance genes, suggesting powerful tools but leaving a gap in grouper-specific, cage-scale characterization of water quality change patterns. At the same time, technological solutions, including portable and automated multi-parameter monitoring devices, are being developed for grouper aquaculture to provide real-time data on temperature, pH, electrical conductivity, and dissolved oxygen, but practical implementation and integration with management decisions remain limited. Consequently, key scientific questions remain regarding the temporal and spatial patterns of water quality change within and around grouper cages, the relative importance of physical, chemical, and biological drivers, and the thresholds at which these changes translate into stress, disease susceptibility, and environmental degradation. Addressing these questions requires systematic monitoring and quantitative analysis of multi-parameter water quality data in operating grouper cage systems, coupled with an understanding of fish physiological responses and surrounding ecosystem processes. By focusing specifically on the characteristics of water quality changes in cage-cultured grouper, the present study aims to provide foundational evidence to guide water quality management, technological monitoring strategies, and eco-friendly farming practices for this economically important species group.

2 Overview of Grouper Cage Aquaculture Systems

2.1 Structure and types of cage farming systems

Modern marine fish farms mainly use open net cages supported by floating collars or platforms, typically circular plastic rings or steel structures that suspend large nets holding tens to hundreds of thousands of fish. These open systems contrast with closed containment tanks, and can themselves be classified into several structural types based on the nature of the supporting frame and containment method. Within open net systems, flexible floating ring cages are common nearshore, while larger rigid platforms and ship-shaped units are being developed for more exposed waters. Increasing interest in offshore and deep-sea cages has driven innovations combining rigid frames with flexible nets to withstand waves and currents and maintain cage volume for fish.

2.2 Environmental characteristics of farming areas

Site hydrodynamics strongly influence suitability for cage farming and water quality around cages. In Kenyan coastal sites, temperature ranged roughly 26°C-33 °C, with deeper, higher-tidal areas showing cooler water and greater column depth, while current speeds and wave heights varied widely between mangrove creeks and open channels (Mirera et al., 2023). These differences mean cage designs and deployment must be tailored to local depth, currents, waves, and shelter conditions. Cage arrays themselves modify surrounding hydrodynamics by adding drag and reducing current speed, which can slow pollutant transport and water exchange. Numerical modeling in the North Yellow Sea showed velocity inside dense cage areas could fall by up to about 45%, creating low-flow zones where solute transport is inhibited and food supply from surrounding waters is reduced (Jiang et al., 2022).

2.3 Stocking density and management practices

Stocking density is a key management lever because it directly shapes growth, feed conversion, survival, and water quality. A review of intensive systems found that excessive densities reduced specific growth rate by 8%-42%, increased feed conversion ratio by 10%-35%, and lowered survival by 5%-28% compared with optimal levels (Firayani, 2024). These biological effects were closely linked to declines in dissolved oxygen and rises in total ammonia nitrogen as biomass and waste loading increased. Field studies in cage farms similarly show that moderate densities often balance yield with fish health and environmental stress. In Lake Victoria cages, densities within a recommended range of 70-150 fish • m⁻³ achieved better growth and health outcomes, whereas sub-optimal higher or lower densities were associated with reduced yields and more frequent fish kills in areas prone to poor water quality (Aura et al., 2025). Similar patterns are reported for other cage-reared species, where lower densities often produce higher individual growth and better survival, underscoring the need to align biomass with the assimilative capacity of the farming site.

3 Key Water Quality Indicator System in Cage Aquaculture

3.1 Physicochemical parameters

Temperature, salinity, dissolved oxygen (DO), and pH form the core physicochemical indicators in cage aquaculture because they directly affect fish metabolism, growth, and survival. Temperature and DO jointly characterize growth conditions, and multivariate analyses in marine aquaculture areas consistently identify them as critical factors for cultured organisms. In a review of fish responses to these variables, shifts in any of these four parameters are described as having strong impacts on physiology, behavior, and population dynamics, emphasizing their role as primary management targets (Mariu et al., 2023).

Field measurements in marine cage and pond systems show that pH typically varies in a narrow range near neutrality or slight alkalinity, while temperature, salinity, and DO exhibit stronger temporal and spatial fluctuations that structure water quality patterns (Zhang et al., 2020). Detailed profiling in commercial sea-cages further reveals substantial three-dimensional variability in temperature and DO within a single cage, with DO occasionally dropping to levels known to limit feed intake and growth, underscoring the need for fine-scale monitoring of these physicochemical indicators.

3.2 Nutrients and organic pollutants

Nitrogen, phosphorus, and organic carbon are key indicators of nutrient loading and organic pollution from cage aquaculture, as uneaten feed and feces are major external inputs. A global review of cage systems estimated that for each ton of fish produced, more than 130 kg of nitrogen and 25 kg of phosphorus can be released to the environment, highlighting cages as important nutrient sources to coastal waters. Mass-balance modeling at bay scale similarly quantified annual releases of over 200 tons of nitrogen and nearly 40 tons of phosphorus from marine cages, confirming that dissolved inorganic forms dominate the nutrient load and can alter ambient nutrient ratios (Figure 1).

Increased nitrogen, phosphorus, and organic matter not only affect the water column but also accumulate in sediments beneath long-term farming areas. Core profiles from semi-enclosed bays show that total nitrogen, total phosphorus, and total organic carbon in surface sediments often exceed safety thresholds, with moderate to severe

pollution linked to prolonged cage farming and low current speed (Cai et al., 2023). Comparative surveys around grouper cages further demonstrate significantly elevated dissolved inorganic nitrogen and soluble reactive phosphorus relative to non-aquaculture waters, identifying these nutrient indicators as central to assessing eutrophication pressure in cage-culture zones (Liu et al., 2024).

Inputs and Fate of Nitrogen (N), Phosphorus (P) and Organic Carbon (OC) in Marine Cage Aquaculture of Groupers

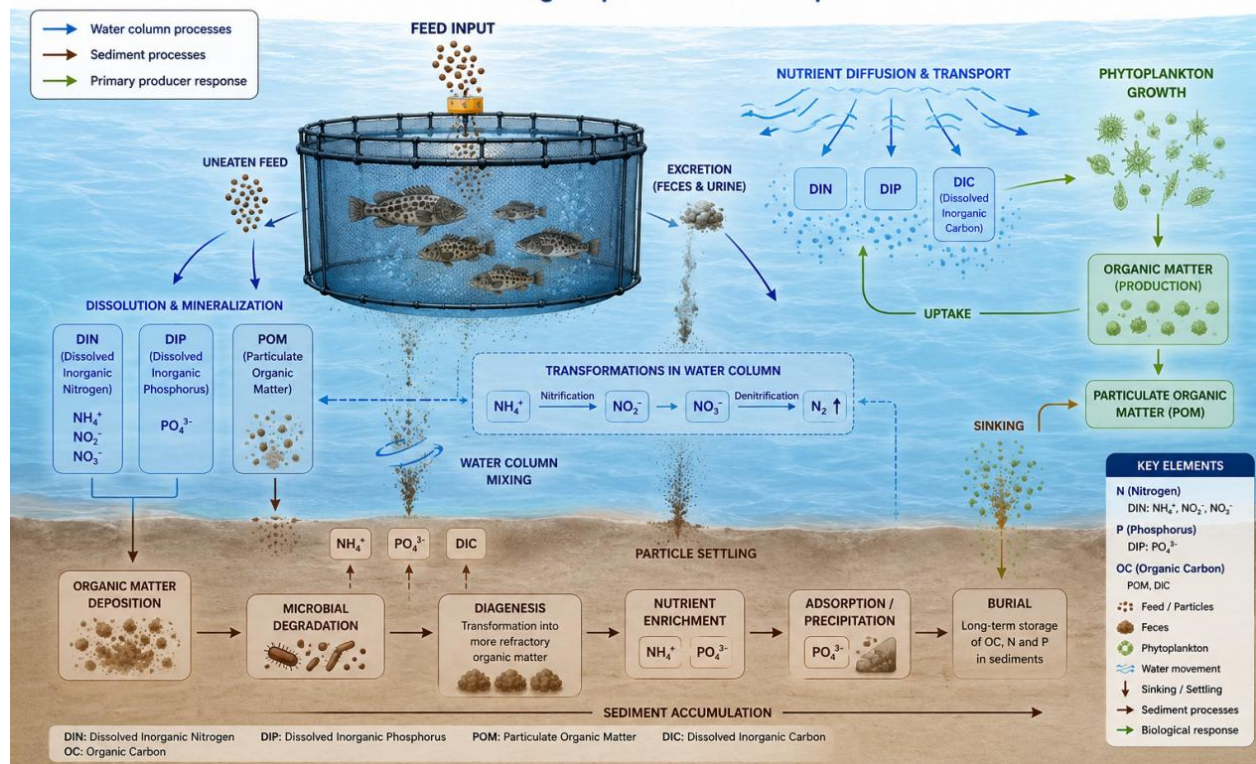


Figure 1 Conceptual pathways of nitrogen, phosphorus, and organic carbon release from grouper cage aquaculture and their transport into the surrounding water column and sediments

Note: Uneaten feed and fish feces are the primary sources of nutrient inputs in cage aquaculture. Released dissolved inorganic nitrogen (DIN), dissolved inorganic phosphorus (DIP), and particulate organic matter (POM) contribute to eutrophication and organic enrichment of sediments

3.3 Biological indicators and microbial community characteristics

Biological indicators, especially microbial communities, provide sensitive and integrative measures of water quality changes in cage aquaculture environments. Comparative metagenomic analysis between grouper cages and nearby non-farmed waters has shown that bacterial diversity and functional genes related to carbon, nitrogen, and sulfur metabolism are significantly altered where eutrophication indicators are elevated (Liu et al., 2024). Correlation analyses indicate that many microbial taxa increase with dissolved inorganic nitrogen and soluble reactive phosphorus but decrease with DO, linking microbial assemblages directly to physicochemical and nutrient indicators.

Beyond planktonic bacteria, broader microbiome-based approaches emphasize microorganisms as both indicators and managers of water quality. Conceptual frameworks propose using shifts in microbial nitrogen and phosphorus transport and metabolism, together with community composition, as early-warning signals of self-pollution and environmental impact in aquaculture systems. Field studies in marine reservoirs with net-cage culture report elevated total heterotrophic bacteria and more frequent detection of fecal indicators such as *Escherichia coli* at cage sites compared with reference locations, illustrating how microbial counts and specific taxa can serve as practical biological indicators of organic loading and contamination in cage-culture waters.

4 Spatiotemporal Variability of Water Quality

4.1 Diurnal variation and tidal forcing mechanisms

Within cage farms, dissolved oxygen (DO) and related parameters often fluctuate markedly over the day-night cycle. Continuous monitoring in seabass cages showed that DO saturation inside cages could be 10%-50% lower than outside, with hypoxic conditions (40%-70% saturation) occurring frequently during summer and autumn. These diurnal patterns were closely linked to fish feeding activity and daily rhythms of plankton, with minimum DO typically coinciding with feeding periods and high temperatures rather than with peak daytime photosynthesis. Tidal currents further modulate short-term DO variability at farm scale. At a commercial salmon farm, tide was the dominant driver of DO levels, producing pronounced differences between up-current and down-current cages during each tidal phase (Burke et al., 2020). As water flowed across the farm, fish respiration and flow restriction acted cumulatively so that downstream cages exhibited substantially lower DO than upstream locations at any given time.

Computational studies show that changes in tidal regime can dramatically alter the duration and volume of low-oxygen water within cage structures. When maximum current speed was halved, or slack tide and tidal cycle length increased, the time that large cage volumes experienced lethal DO levels (<30% of ambient) increased from near zero to more than an hour (Nguyen et al., 2025). These findings highlight the interaction between fish density, current speed, and tidal characteristics in controlling diurnal DO risk and emphasize the need to adjust stocking density to local tidal dynamics.

4.2 Seasonal variation patterns

Seasonal forcing generates strong temporal patterns in cage-area water quality, often through changes in temperature, stratification, and primary productivity. In a seabream cage farm off Oman, summer surface temperatures reached ~32 °C and extended hypoxia developed below 35 m, whereas winter conditions were more vertically homogeneous and less extreme. Short up- or down-welling events driven by energetic flow pulses broke stratification and caused rapid shifts in temperature and oxygen, underscoring the importance of seasonal mixing dynamics for farm management (Al-Yahyai et al., 2020). Multivariate analyses of marine aquaculture areas in northern China also demonstrate pronounced seasonal changes in water quality. In a cage culture area, principal component scores indicated that overall pollution burden peaked in November, when declining temperature, reduced primary productivity, and intensive harvest activities coincided to elevate key indicators.

In contrast, summer conditions with strong light and suitable temperatures favored phytoplankton growth and nutrient drawdown, leading to relatively lower nutrient concentrations despite high biological activity (Zhang et al., 2020). In inland and reservoir cage systems, seasonality similarly shapes key limnological variables. In a large Brazilian reservoir, PCA of a multi-year dataset around a great-volume cage system revealed two phases: a pre-farming period characterized by higher DO and temperatures, and a post-production period marked by elevated ammonium and total phosphorus, with these shifts strongly influenced by seasonal hydrology (Rosini et al., 2019). Seasonal rainfall further reduced transparency by transporting allochthonous material and suspended solids, decoupling clarity from phytoplankton abundance.

4.3 Spatial heterogeneity and distribution characteristics

At the scale of individual farms, water quality often varies between cage and reference sites as well as along flow paths. In a tropical marine cage farm, nutrient concentrations and chlorophyll *a* were generally higher than in pristine environments, but temperature, salinity, DO, and pH did not differ significantly between stations near and away from cages over a year. This pattern suggests that high organic loading can elevate nutrients and bacterial abundance without always producing strong horizontal gradients in basic physico-chemical parameters. Other systems show clearer horizontal gradients related to farm location and broader limnological context. In Lake Victoria, water transparency increased and nutrient loading decreased with distance from eutrophic inner gulf sites toward more oligotrophic open-lake areas, forming a strong regional gradient that overshadowed local cage-control differences (Okechi et al., 2022). Despite higher fish biomass near cages, principal component scores for eutrophication and seasonal variability did not differ significantly between paired cage and control stations at any site.

Spatial comparisons across multiple mariculture systems reveal that system type and layout also influence water quality patterns. In a Chinese coastal region containing seaweed, shellfish, and cage-fish areas, DO and transparency were relatively higher in seaweed zones, while nutrient concentrations were elevated in cage fish and shellfish areas compared with a blank control, indicating distinct local water quality signatures for each system (Zhu et al., 2023). Principal component and redundancy analyses further linked spatial differences in phytoplankton composition to gradients in total nitrogen, salinity, and transparency, illustrating how physical and chemical heterogeneity structures biological communities within and among farming areas.

5 Mechanisms of Aquaculture Activities Affecting Water Quality

5.1 Feed input and residual feed decomposition processes

In cage-culture systems, feed is the primary input of nutrients and organic matter, and a considerable fraction is not converted into fish biomass but lost as uneaten pellets and associated particulates. Mass-balance analyses show that only about 39%-43% of feed nitrogen and phosphorus are retained in salmon tissues, with the remainder released as organic particulates and dissolved wastes (Wang and Olsen, 2023). Conceptual nutrient budgets for cage aquaculture similarly indicate that on the order of 130 kg •N and 25 kg •P can be discharged per ton of fish produced, emphasizing the central role of feed inefficiency in nutrient emissions.

Uneaten feed that sinks below cages undergoes mineralization, releasing dissolved inorganic nitrogen and phosphorus and contributing to eutrophication, oxygen depletion, and increased biological oxygen demand. Studies in floating net cages report that 20%-30% of feed is uneaten and partially decomposes in the water, becoming a major source of nitrogen, phosphorus, and organic matter pollution (Astuti et al., 2023). Reviews of aqua-feed wastes further note that the dietary composition of feeds governs the proportion and form of nitrogenous and phosphorus compounds entering the environment, which in turn drive changes in pH, algal turbidity, and eutrophication risk.

5.2 Waste excretion and organic load accumulation

Beyond uneaten feed, fish metabolism generates substantial dissolved and particulate wastes that accumulate in and around cages. Mass-balance models for Atlantic salmon indicate that approximately 18% of consumed carbon, nitrogen, and phosphorus is lost as defecation, while 39%-43% is released through excretion or respiration, underscoring the importance of metabolic pathways in waste generation. Similar modeling approaches for cage farms estimate that over 60% of phosphorus waste is solid, whereas more than 65% of nitrogen waste is excreted as dissolved ammonia, illustrating how excretion loads the water column with reactive nitrogen.

These waste fluxes can alter water and sediment chemistry when they exceed local assimilative capacity. In a eutrophic lake with Nile tilapia cages, increased concentrations of nitrogen and phosphorus near cages stimulated algal growth, while organic material accumulated beneath cages elevated benthic biochemical oxygen demand and promoted anoxic conditions and reduced redox potential (Musa et al., 2022). A broader review of aquaculture wastewater confirms that aquafeed, drugs, and metabolic wastes collectively contribute conventional pollutants and organic compounds to receiving waters, requiring improved treatment and management to avoid long-term environmental and health risks (Liu et al., 2024).

5.3 Biological disturbance and ecological feedback effects

Organic enrichment from feed and wastes modifies benthic habitats, driving biological disturbance and feedbacks on water quality. Case studies around Mediterranean fish farms show that sediments beneath cages experience biodiversity loss and are dominated by opportunistic species such as *Capitella* sp. I, with the impact generally confined to tens of meters but closely linked to cultured biomass and hydrodynamic conditions. Similar patterns appear in tropical environments, where elevated organic waste deposition directly beneath and adjacent to cages leads to highly perturbed macrobenthic communities with extremely low diversity and dominance of second-order opportunists (Grouazel et al., 2025).

Bioturbation and bioirrigation by benthic fauna can partially moderate these impacts, but also alter ecosystem functioning near farms. Work at the edge of an allowable zone of effect found that higher bioturbation potential near cages reshaped microphytobenthic communities and trophic structure, shifting dominance toward euglenophytes and scavenging macrofauna while still supporting diverse trait combinations. Long-term observations of meiofaunal recovery after farm removal indicate that, although densities may begin to rebound within months, community structure and taxa richness remain altered, revealing time-lagged ecological feedbacks between past organic loading, benthic communities, and subsequent ecosystem resilience.

6 External Environmental Drivers of Water Quality Dynamics

6.1 Ocean hydrodynamic exchange processes

Ocean hydrodynamics govern how wastes and nutrients from cage-cultured grouper are diluted, transported, or retained around farms. Numerical simulations in the North Yellow Sea showed that suspended cages create low-velocity zones inside farm areas, with current speed reduced by up to about 45% under high-density culture, which in turn inhibits pollutant transport away from cages (Jiang et al., 2022). Similar modeling work in Sansha Bay found that near-surface current speed in cage-free areas was more than three times that inside cage areas in deep channels, indicating strong cage-induced drag that can slow horizontal water exchange.

Three-dimensional hydrodynamic studies further show that cages modify both horizontal and vertical flow structures, affecting the dispersion of dissolved and particulate effluents. High-resolution modelling demonstrated complex perturbations to tidal flows around cage arrays and revealed that altered currents strongly influence redistribution of passive tracers such as feed, faeces, or dissolved markers through and within cages. Observations in a semi-enclosed bay similarly identified a “double-drag” structure, with cage-induced surface friction reducing current velocities by up to 54% and hindering horizontal water exchange, while enhanced shear and turbulence below cages locally improved vertical mixing (Figure 2) (Jiang et al., 2022).

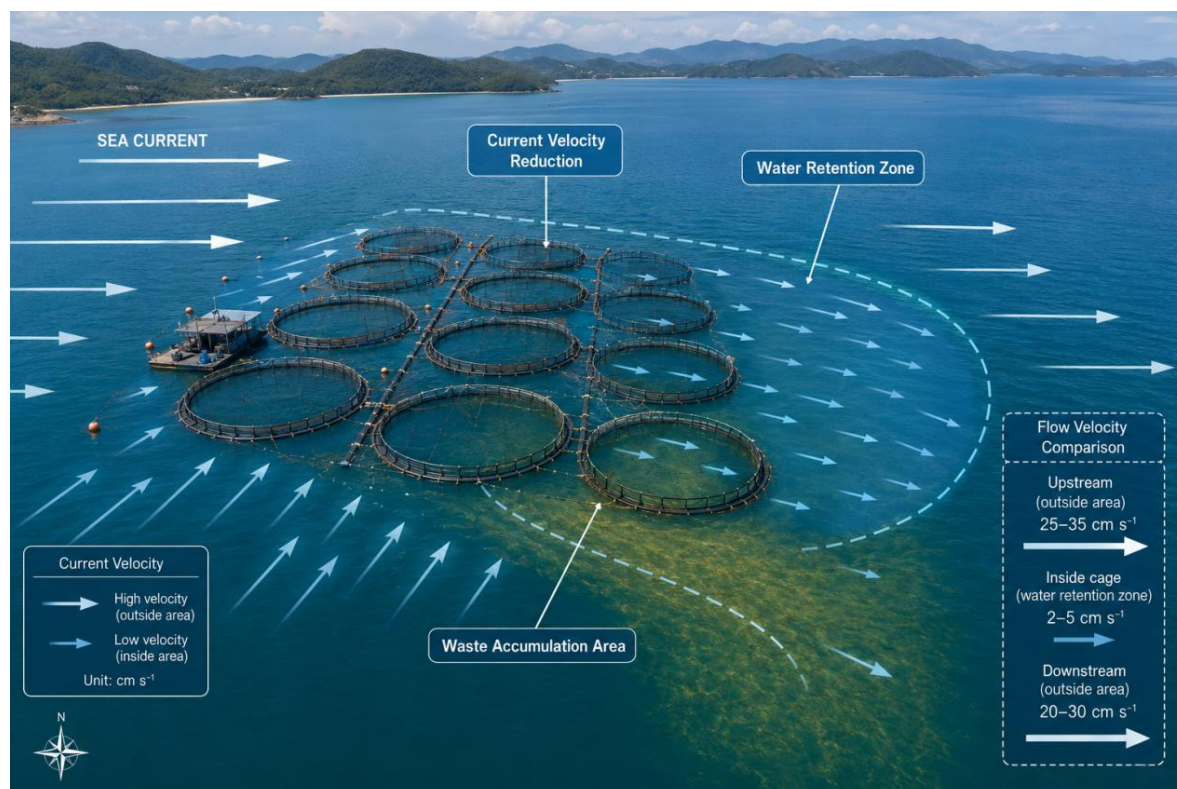


Figure 2 Hydrodynamic interaction between grouper cage arrays and surrounding coastal waters

Note: Cage structures obstruct water movement and create low-velocity zones within farming areas. Reduced current speeds increase water retention and may promote local accumulation of nutrients and organic wastes

6.2 Meteorological influences

Meteorological forcing alters stratification, circulation, and external inputs, thereby reshaping water quality around cage farms. Remote-sensing analysis of Typhoon In-fa in the Zhoushan fishery showed that strong vertical mixing from the typhoon led to a marked decrease in sea surface temperature, with more intense cooling on the right side of the track due to asymmetric wind stress and pre-existing temperature structure (Tang et al., 2023). Despite mixing and inflow of hypersaline water, intense rainfall and diluted water input caused an overall post-typhoon decrease in sea surface salinity, illustrating how wind and rain jointly modify the hydrographic context in which cages operate.

Typhoons also directly affect wave and current regimes, with implications for cage integrity and water exchange. Simulation of typhoon Rammasun in Maniao Bay predicted that during the storm, significant wave height in the cage area exceeded 5.5 m and maximum flow velocity reached about $1.5 \text{ m} \cdot \text{s}^{-1}$, surpassing the design carrying capacity of deep-water cages and leading to potential deformation or damage (Zhang et al., 2024). Broader reviews of mariculture net-cage disasters in China emphasize that strong winds and waves associated with typhoons can cause overtopping, frame collapse, and structural instability, producing abrupt changes in the rearing environment that depress growth and increase disease and escape risk.

6.3 Pollution inputs from surrounding marine areas

External pollution inputs from the wider marine environment interact with farm-derived wastes to shape water quality in cage-culture zones. An evaluation of marine aquaculture areas using principal component analysis showed that in cage regions, chlorophyll a, salinity, and dissolved oxygen were dominant factors, while antibiotic resistance genes (ARGs) appeared more diverse and frequent in cages than ponds, suggesting terrestrial inputs contribute to pollution signatures beyond farm discharges alone. In Lake Victoria, comparisons along a strong background eutrophication gradient indicated that terrestrial and other non-cage sources were the major drivers of gulf-wide nutrient enrichment, with cage farms showing no significantly higher nutrient enrichment or turbidity than ambient conditions at paired control sites (Okechi et al., 2022).

At the same time, cumulative nutrient outputs from multiple farms can contribute substantially to regional nutrient budgets and interact with external sources. A global synthesis estimated that each ton of fish produced in marine cages releases on the order of $132.5 \text{ kg} \cdot \text{Nitrogen}$ and $25 \text{ kg} \cdot \text{Phosphorus}$, raising concern that additive discharges from many farms, together with other coastal inputs, may enhance primary production and eutrophication in intensively farmed regions. Long-term analysis in Sansha Bay quantified large percentage increases in sediment heavy metals and substantial enhancements of dissolved inorganic nitrogen and phosphorus attributable to cage culture compared with conservative mixing, demonstrating how aquaculture activities amplify contamination on top of natural and external background processes in semi-enclosed coastal systems (Song et al., 2023).

7 Case Study: Water Quality Dynamics in a Typical Grouper Cage Aquaculture Area

7.1 Study area description and monitoring design

A representative example of grouper cage aquaculture is found in Xincun Port, Lingshui County (Hainan, China), where fixed marine cages dominate the sheltered inner bay. All sampling sites in the aquaculture area are fixed cages with the net body extending 0.7-1.0 m above the surface and 1.5-2.5 m below, stocked exclusively with giant grouper (*Epinephelus lanceolatus*). The farming zone is embedded within a semi-enclosed port that also contains nearby non-aquaculture waters, providing a natural reference for assessing aquaculture impacts under similar hydrological conditions (Liu et al., 2024).

Water quality monitoring in this case followed an integrated design combining in situ profiling and laboratory analyses. Surface water (~1 m depth) was sampled once in May from three aquaculture cages and three non-aquaculture sites, with temperature, dissolved oxygen, conductivity, salinity, redox potential and pH measured immediately using a handheld multiparameter meter. Bulk water was then filtered for colorimetric determination of ammonium, nitrite, nitrate and soluble reactive phosphorus, allowing calculation of dissolved inorganic nitrogen and construction of a multi-indicator dataset linking physicochemical conditions to microbial communities.

7.2 Observed water quality dynamics

Comparisons between grouper cages and nearby reference waters revealed pronounced differences in nutrient status and eutrophication indicators. Dissolved inorganic nitrogen and soluble reactive phosphorus were significantly higher in aquaculture waters, indicating enhanced nutrient loading associated with feed inputs and metabolic wastes (Liu et al., 2024). These nutrient enrichments occurred despite the relatively small vertical extent of the cages, suggesting that even shallow water columns can accumulate substantial dissolved nutrients when flushing is limited.

Patterns observed in this grouper system are consistent with broader analyses of marine cage aquaculture areas. In a northern China marine farming region, multiseason sampling at 19 sites showed that chlorophyll a, salinity, dissolved oxygen and inorganic nitrogen dominated principal components for cage areas, with the heaviest pollution occurring in November when aquaculture activity and seasonal conditions combined to elevate scores. These results indicate that nutrient enrichment and oxygen dynamics in cage systems show both spatial contrasts with nearby non-aquaculture zones and marked temporal variability linked to farming operations and seasonality.

7.3 Relationship between aquaculture activities and environmental responses

The grouper case study demonstrates clear coupling between aquaculture practices and environmental responses. Elevated nutrients and eutrophication indicators in cages relative to adjacent waters coincide with significant shifts in planktonic bacterial communities, including increased abundances of *Vibrio* and *Pseudoalteromonas* and altered functional genes for carbon, nitrogen and sulfur metabolism. Correlation analyses show that many taxa respond positively to dissolved inorganic nitrogen and soluble reactive phosphorus but negatively to dissolved oxygen, indicating that nutrient enrichment and oxygen stress jointly structure microbial assemblages in grouper cages.

Similar linkages between aquaculture pressure and water quality emerge at larger spatial and temporal scales. In the Zhuanghe marine aquaculture region, principal component analysis integrating pH, temperature, salinity, dissolved oxygen, nutrients, chlorophyll a, chemical oxygen demand and antibiotic resistance genes identified aquaculture activities and seasonality as the main drivers of water quality in cage areas (Zhang et al., 2020). Moreover, cage areas showed higher variety and frequency of antibiotic resistance genes than pond systems, suggesting additional environmental stressors linked to terrestrial inputs and farm management. Together, these findings highlight that feed inputs, stocking practices, and ancillary inputs in grouper cage aquaculture not only alter classical physicochemical indicators but also drive complex microbial and genetic responses in the surrounding environment.

8 Impacts of Water Quality Changes on Grouper Health and Growth

8.1 Stress responses and physiological metabolism changes

Water quality directly shapes stress status and metabolic regulation in grouper, with several studies highlighting specific pathways. Elevated unionized ammonia causes hematological depression, oxidative stress, and increased stress indicators such as plasma cholesterol and heat shock protein 70 in juvenile hybrid grouper, demonstrating systemic physiological disruption under poor water quality. Combined hypoxia and ammonia exposure further elevates oxygen consumption and activates genes involved in glucose and amino acid metabolism, indicating that co-occurring stressors substantially increase energetic costs to maintain homeostasis (Cao et al., 2024).

Other water-quality-related stressors, particularly temperature fluctuation, alter metabolic profiles at molecular and organismal levels. Mucus and serum metabolomics under temperature fluctuation stress identified disturbances in purine metabolism, TCA cycle, and methionine and pyruvate metabolism in juvenile hybrid grouper, differentiating susceptible from resilient phenotypes. Elevated temperature (33 °C-36 °C) over 14 days significantly reduced body weight, suppressed antioxidant enzymes, and altered digestive enzyme activities, with high-temperature exposure classified as a high-stress level by a quantitative hazard system.

8.2 Disease occurrence and links to water quality

Suboptimal water quality can aggravate disease outcomes, even when basic parameters remain within nominal ranges. In humpback grouper cages infected by viral nervous necrosis (VNN), measured temperature, pH, dissolved oxygen, salinity, nitrate, and phosphate stayed within values considered normal for the species, yet fish showed

severe clinical signs and high mortality, indicating that poor water quality mainly increases stress and susceptibility rather than acting as the sole cause of infection. A broader systematic review of marine cage culture in East and Southeast Asia notes that environmental triggers, including water quality deterioration, are important in initiating outbreaks of *Vibrio* spp., parasitic infections, and viral diseases such as iridoviruses and nervous necrosis virus (Jahangiri et al., 2022).

Quantitative farm-level data link specific water quality variables to pathogen presence in cage-cultured grouper. A survey of marine cages found multiple co-occurring pathogens, including *Vibrio alginolyticus*, *V. vulnificus*, *Photobacterium damsela*, nervous necrosis virus, and iridovirus, and identified water temperature, dissolved oxygen, ammonia, iron, and nitrite as the most significant physicochemical factors associated with their occurrence. A review of fish health aspects in grouper culture further emphasizes that environmental deterioration and intensive practices contribute to frequent viral, bacterial, and parasitic disease problems, complicating large-scale production (Figure 3).

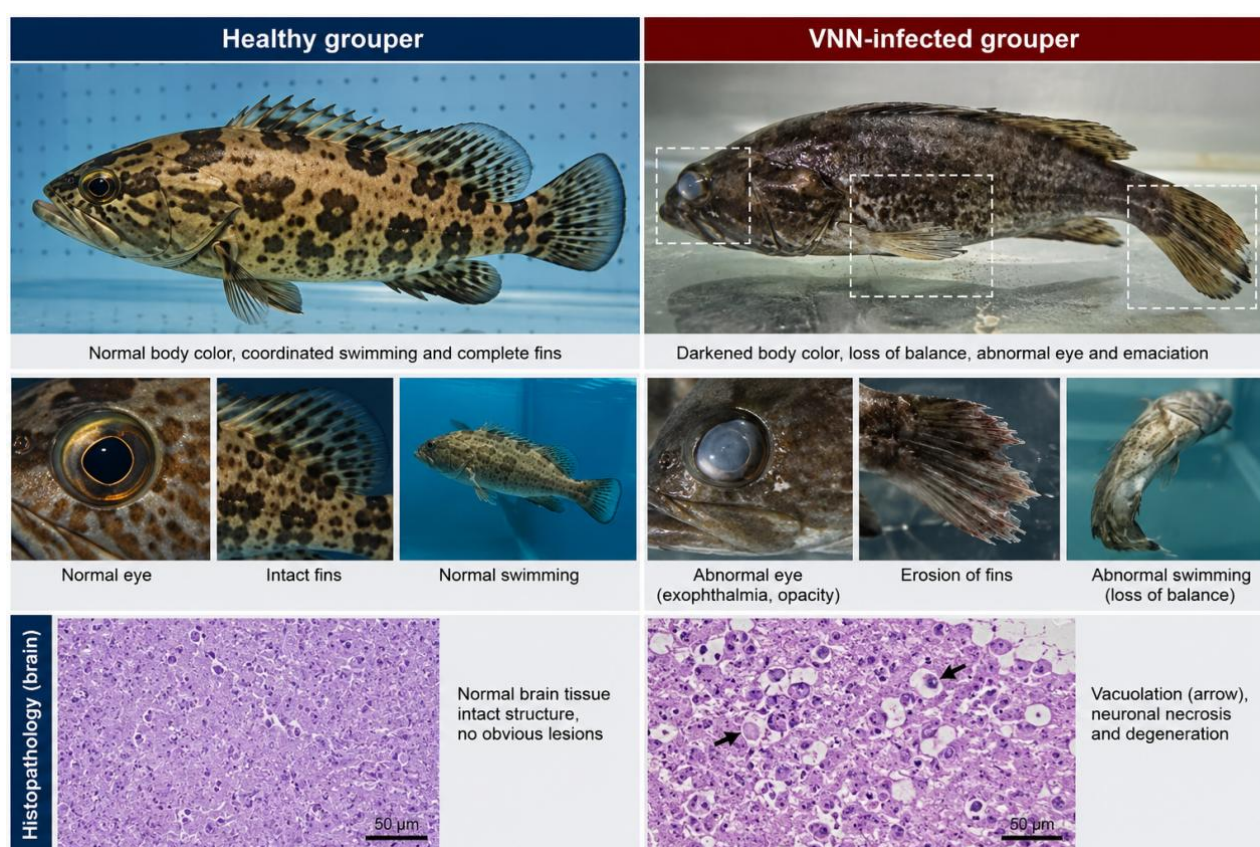


Figure 3 Representative clinical signs observed in healthy and diseased cage-cultured grouper

8.3 Growth performance and survival rate variations

Water quality management regimes strongly influence grouper growth and survival outcomes. In a 40-day nursery trial comparing flow-through, recirculation, and recirculation with bioremediation, the bioremediation treatment achieved the most stable salinity and ammonia ranges and inhibited *Vibrio* spp., yielding the highest survival (94.8 %), fastest length and weight growth, and lowest feed conversion ratio (Ismi et al., 2023). Similarly, combining water exchange with siphoning in hybrid grouper culture improved water quality by reducing ammonia, phosphate, and total organic matter, and achieved 100 % survival and better feed utilization than treatments with poorer waste removal (Putra et al., 2025).

Specific water quality parameters also determine growth efficiency and mortality risk. Cage experiments with tiger grouper under different salinities showed that 32 psu produced the highest absolute and specific growth rates and survival, along with the most favorable feed conversion ratio, whereas lower salinities reduced survival. In

multitrophic microcosms, brown-marbled grouper survival (47%-87%) was lower than previous reports despite generally acceptable temperature, salinity, and pH, and high ammonia and phosphate concentrations were identified as likely causes of the reduced survival, highlighting the lethal impact of nutrient accumulation even when other parameters appear adequate. Water quality regulation is central to sustaining cage-cultured grouper, as intensive feeding, high stocking densities, and constrained hydrodynamics can rapidly drive eutrophication, oxygen depletion, and disease. This section outlines strategies that align ecological carrying capacity, real-time control, and green technologies to maintain stable water conditions while supporting viable production.

9 Water Quality Regulation and Management Optimization Strategies

Ecological regulation in cage-cultured grouper begins with matching farming intensity to the assimilative capacity of surrounding waters. Studies on cage aquaculture show that exceeding environmental carrying capacity leads to nutrient accumulation, algal blooms, and benthic degradation, directly undermining fish health and long-term productivity. Carrying capacity can be estimated using mass-balance or Bayesian models that link allowable biomass to key indicators such as chlorophyll-a, particulate nitrogen, and hydrodynamics. In practice, this translates into limits on total biomass, cage number, and stocking density per farming zone, combined with strict control of feed inputs and phosphorus content to restrain eutrophication. Spatial planning is equally important for grouper cages. Hydrodynamic-based site selection favors areas with sufficient depth and current speeds that disperse wastes without exporting impacts to sensitive habitats or conflicting water users. Zoning and registration systems that concentrate cages in designated areas, cap total units, and remove illegal or excessive structures help keep production within ecological limits and reduce conflicts over water use. Within farms, better management practices-optimized stocking density, phased fallowing, and selective adoption of semi-intensive over highly intensive feeding regimes-can maintain acceptable dissolved oxygen, ammonia, and organic loading while sustaining economic returns. Community-based governance frameworks further support compliance and adaptive adjustment of carrying capacity thresholds as environmental conditions change.

Real-time monitoring systems have become indispensable for managing water quality dynamics around grouper cages. Sensor-based platforms using microcontrollers, wireless communication, and low-cost probes can continuously track temperature, dissolved oxygen, pH, turbidity, and salinity at relevant depths. Unlike manual sampling, these systems provide high-frequency data, allowing early detection of hypoxia, acidification, or turbidity spikes linked to storms, floods, or operational failures. Calibration against reference instruments and protective sensor housings improve accuracy and durability, making such systems suitable for prolonged deployment in coastal and offshore environments. Early warning functions transform raw monitoring data into actionable management responses. Threshold-based alerts delivered via SMS, mobile apps, or IoT dashboards notify farmers when parameters deviate from safe ranges, enabling rapid interventions such as adjusting feeding, aeration, or cage depth. In rivers and reservoirs, distributed sensor nodes tracking water level, flow velocity, and turbidity can warn of approaching flood events hours in advance, reducing cage losses and escape events. AI-enabled buoy systems and cloud platforms extend these capabilities by analyzing trends, predicting short-term changes in temperature or current velocity, and supporting decision rules for stocking, harvest timing, and emergency response. For grouper farms, integrating these technologies supports more precise feeding, reduces stress-related mortality, and stabilizes water quality under increasingly variable climatic and anthropogenic pressures.

Green aquaculture for cage-cultured grouper focuses on closing nutrient loops, cutting waste emissions, and lowering the carbon footprint of production. Nutrient budgeting has shown that conventional cages release substantial nitrogen and phosphorus per tonne of fish, driving eutrophication when unmanaged. Integrated multitrophic aquaculture (IMTA), aquaponics, and loop bio-phytoremediation systems offer effective remedies by coupling fed species with extractive organisms. Co-culturing fish with bivalves, macroalgae, or filter-feeding invertebrates enhances nutrient retention, while hydroponic or wetland plants remove dissolved inorganic nitrogen and phosphorus from recirculated water with high efficiency. Field systems combining floating net cages, physical filters, and phytoremediation plants have achieved large reductions in nitrate, phosphorus, and organic matter discharged to surrounding waters. At the pond and system scale, IMTA-aquaponic configurations have improved

feed conversion ratios and raised nitrogen and phosphorus utilization above 80%, transforming fish waste into additional biomass of finfish, shellfish, and vegetables. For marine grouper systems, floating treatment wetlands planted with halophytic species can simultaneously lower dissolved inorganic nitrogen and reduce CO₂ and N₂O emissions, providing co-benefits for water quality and greenhouse gas mitigation. Complementary measures include reformulation of feeds to reduce phosphorus content without compromising growth, optimization of stocking density to balance production and stress, and adoption of energy-efficient equipment to curb fuel and electricity use. Together, these green technologies and emission-reduction practices reposition grouper cage culture on a trajectory that aligns productivity with ecological resilience and climate goals. Maintaining suitable water quality in cage-cultured grouper requires aligning production intensity with ecological carrying capacity, supported by spatial planning and robust farm-level practices. Real-time monitoring and early warning systems enable rapid responses to environmental fluctuations and operational risks. Green technologies-ranging from IMTA and phytoremediation to low-phosphorus feeds and energy-efficient operations-substantially reduce nutrient emissions and greenhouse gas outputs, creating a more sustainable and resilient grouper aquaculture sector.

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Conflict of Interest Disclosure

The authors affirm 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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