

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.

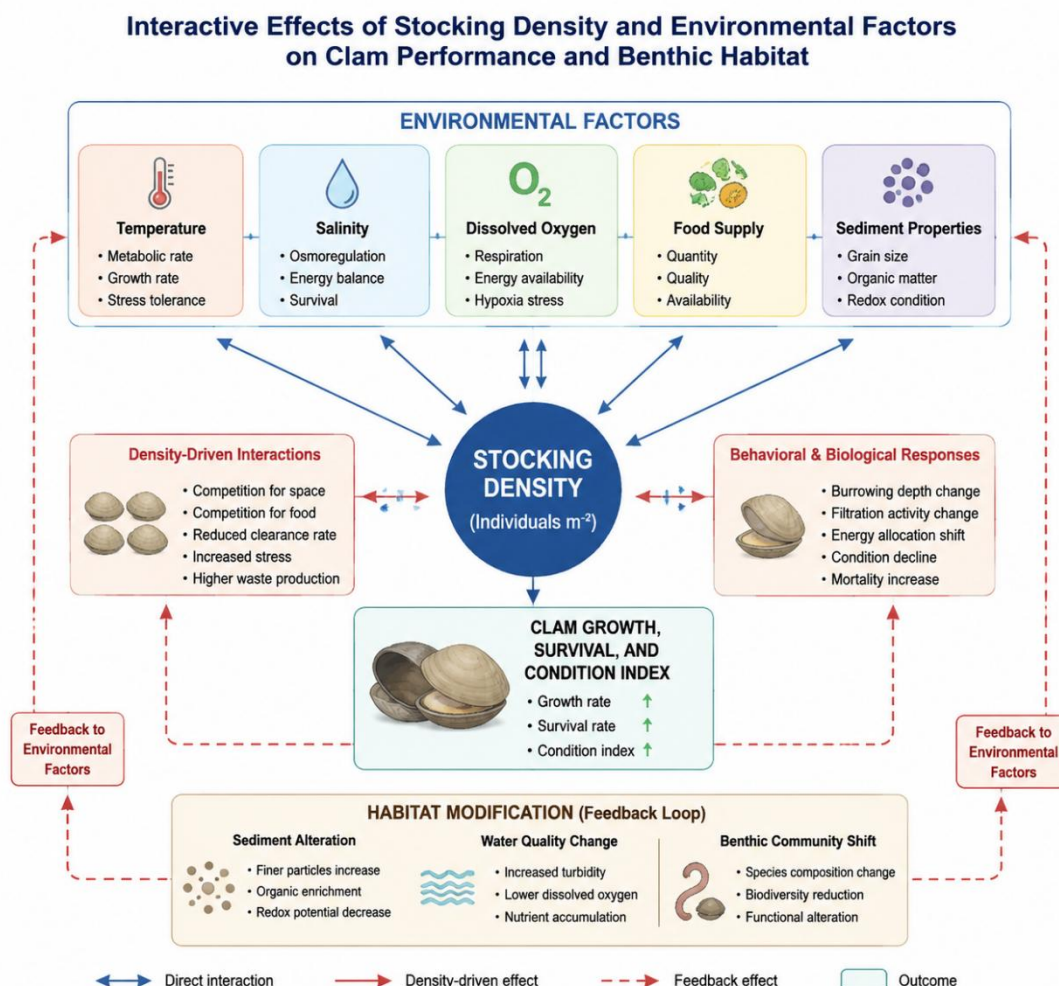


Figure 1 Conceptual framework illustrating the interactive effects of stocking density and environmental factors on clam performance and benthic habitat conditions

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

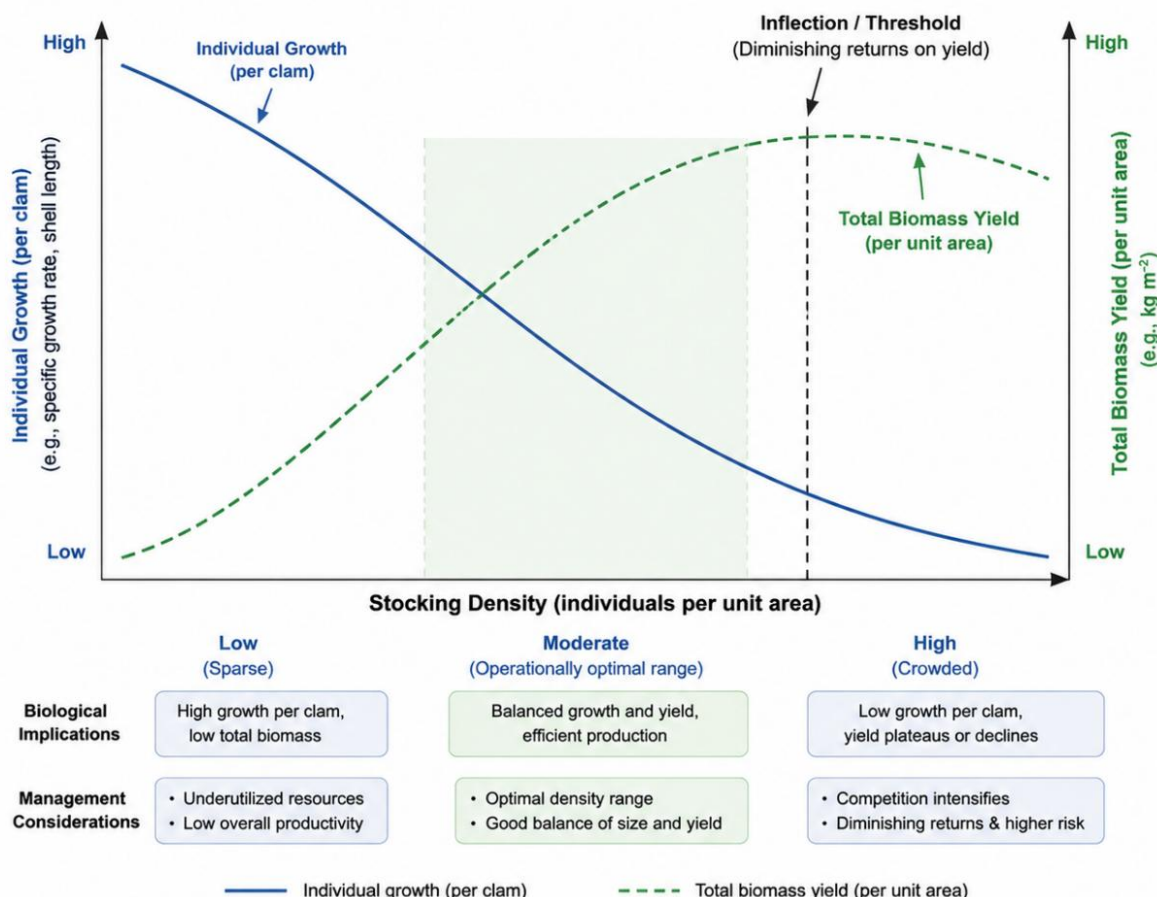


Figure 2 Conceptual trade-off between stocking density, individual growth, and total biomass yield in Manila clam culture systems

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.

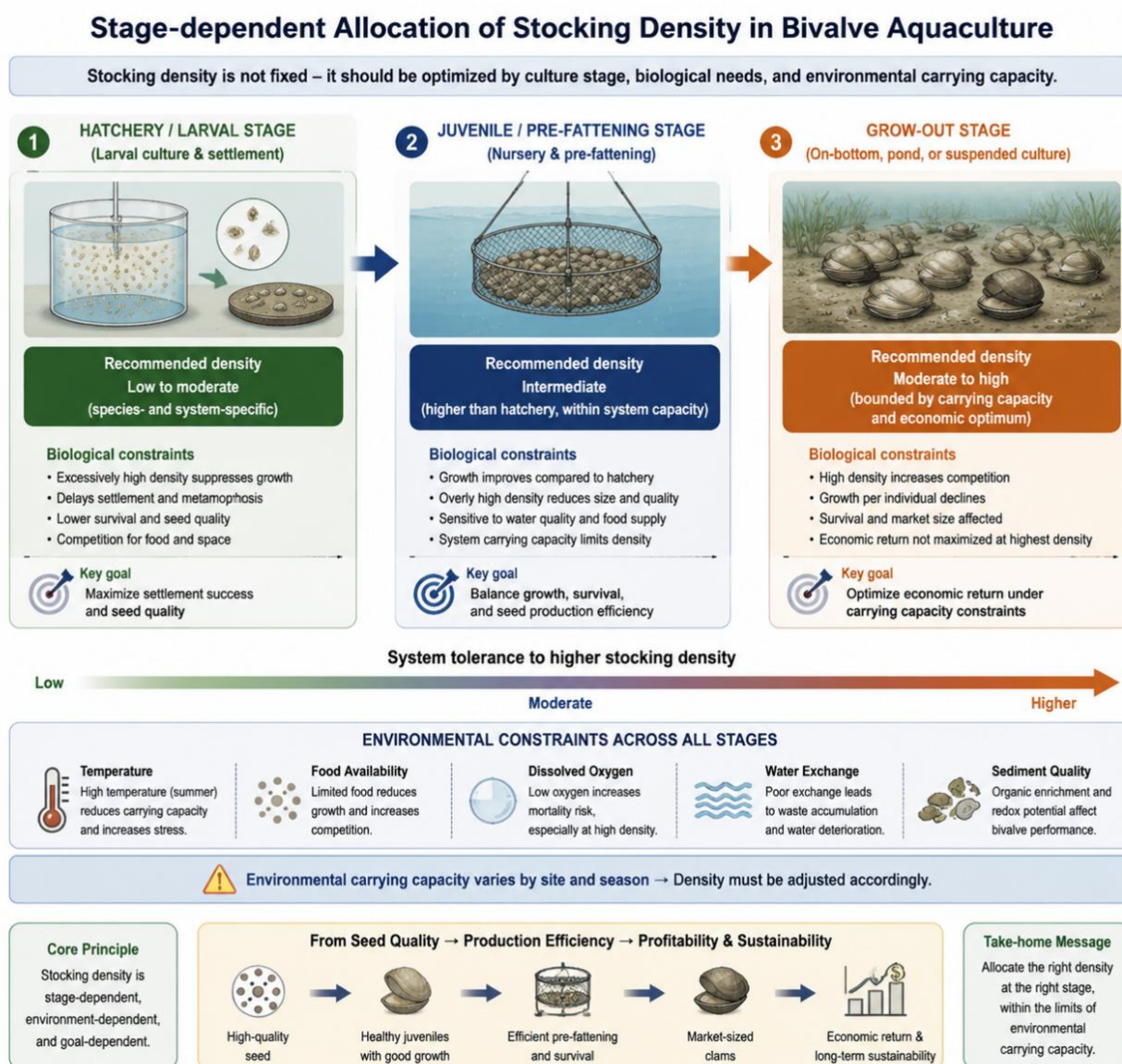


Figure 3 Stage-dependent allocation framework of stocking density across hatchery, juvenile, and grow-out phases in bivalve aquaculture systems

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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