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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.

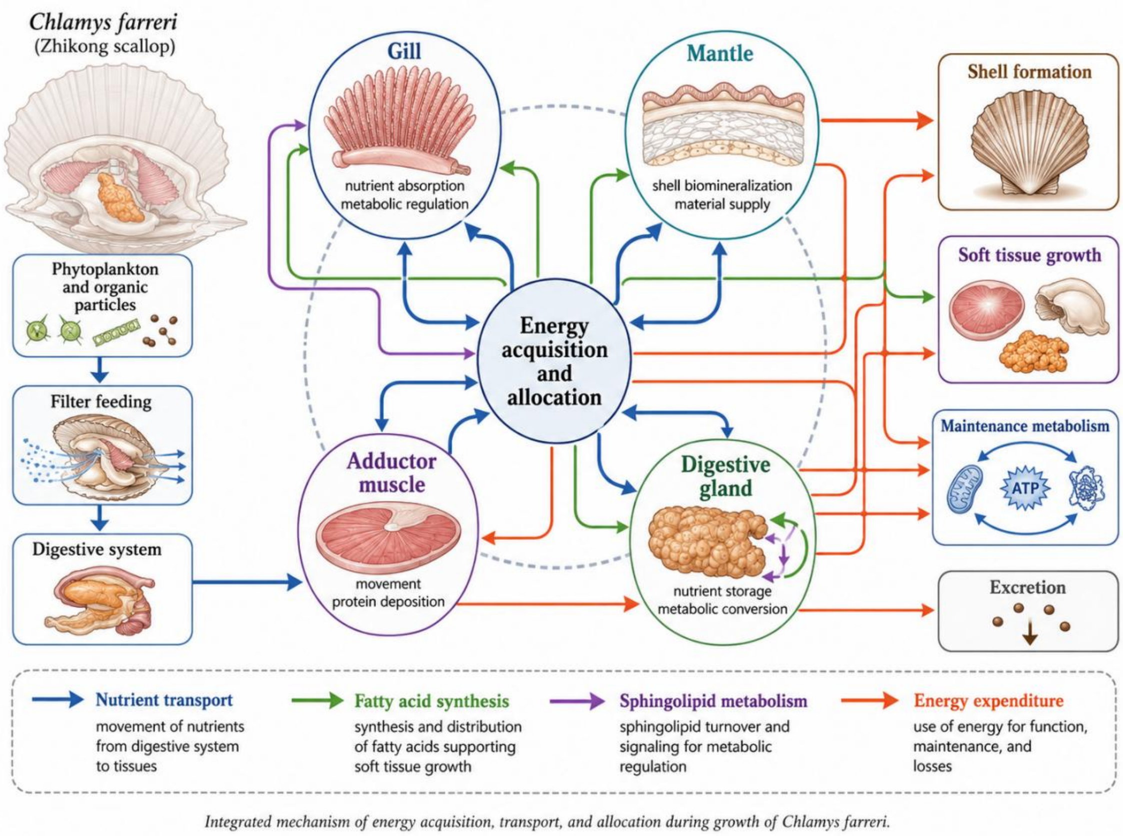

Figure 1 Conceptual model of energy acquisition, tissue-specific metabolism, and growth allocation in Chlamys farreri. Energy obtained from filtration feeding is distributed among shell formation, soft tissue growth, maintenance metabolism, and excretion through coordinated functions of the gill, mantle,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

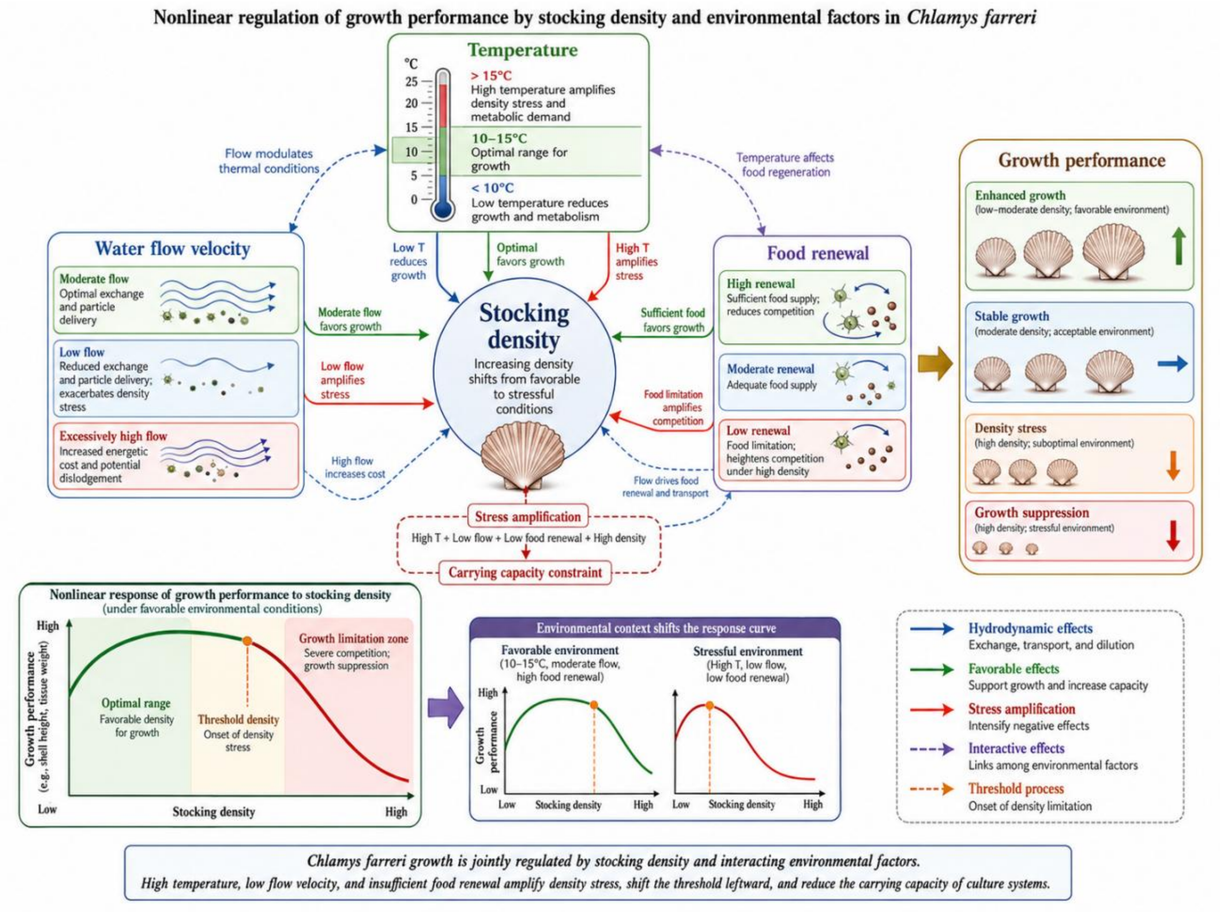

Figure 2 Conceptual framework illustrating the interactive effects of stocking density, temperature, hydrodynamics, and food availability on scallop growth. Environmental conditions modify density-dependent responses by regulating food renewal, metabolic demand, and ecological thresholds

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.

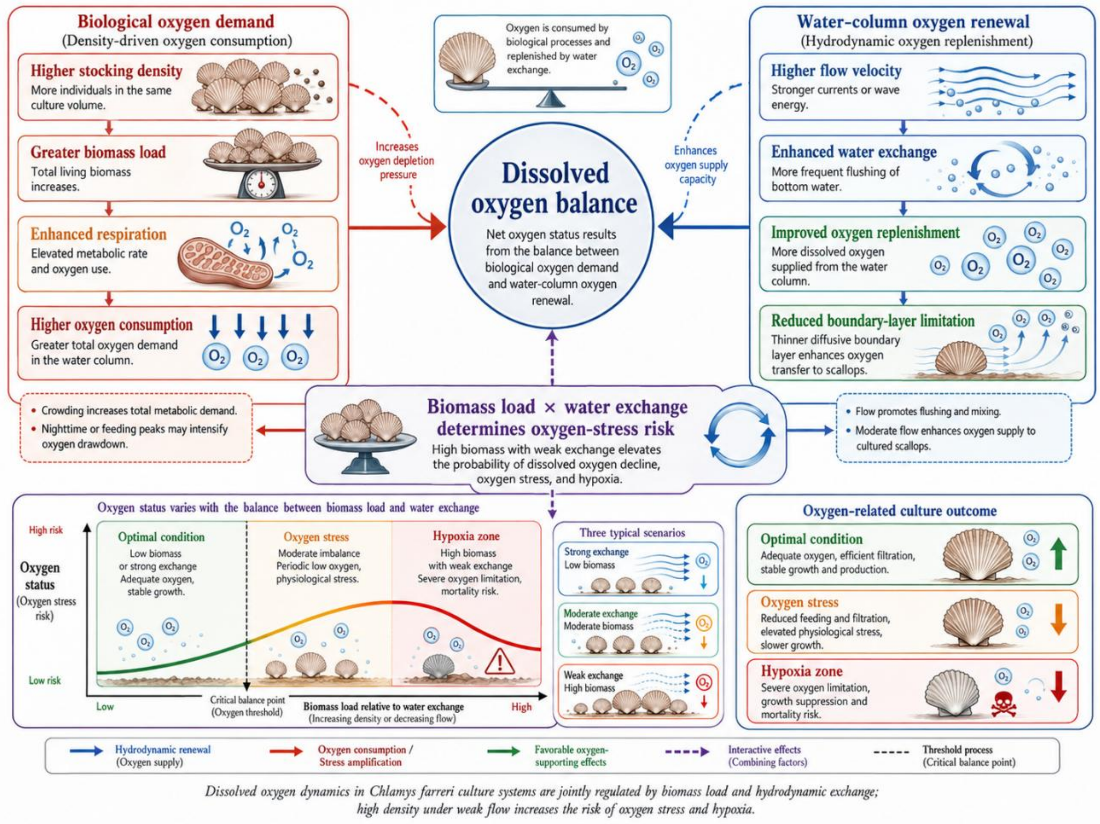

Figure 3 Conceptual model illustrating the coupled effects of stocking density and water exchange on dissolved oxygen dynamics in scallop aquaculture systems. Oxygen availability is determined by the balance between biological oxygen demand and hydrodynamic oxygen renewal

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 mm^3/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 $g \cdot m^{-2}$, 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 Sungo 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 Sungo 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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