

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).