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Mussel ecosystem services increased by triploidy

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Abstract

Filter-feeding bivalves represent a significant area of aquaculture development and are widely recognized for their valuable ecosystem services. They are considered extractive species, capable of capturing excess nutrients from the environment and converting them into nutritious food for human consumption. Triploidy has been widely used in the oyster industry to enhance production, as triploid oysters allocate most of their energy toward growth. However, the reported productivity gains remain contentious, with some studies indicating that triploidy confers no significant advantage or disadvantage. This approach could also be applied to other shellfish species to boost productivity and improve other energy-dependent processes, such as byssogenesis in mussels. Mussels are one of the most extensively cultivated shellfish species globally and play a significant economic role in coastal regions of Canada. A major challenge in suspension-cultured mussel farming is the high rate of mussel fall-off from cultivation ropes, which reduces harvest yields. Additionally, mussel detachment affects the ecosystem services provided by these filter-feeding organisms in coastal habitats. Mussels remain attached in suspension culture through byssal thread production, a crucial attachment mechanism. Weak byssal thread attachment is a key factor contributing to detachment, and various environmental and biological factors influence this process. This review explores advancements in shellfish productivity through the use of triploidy and examines how this management strategy could be leveraged to enhance byssal attachment capacity in mussels.

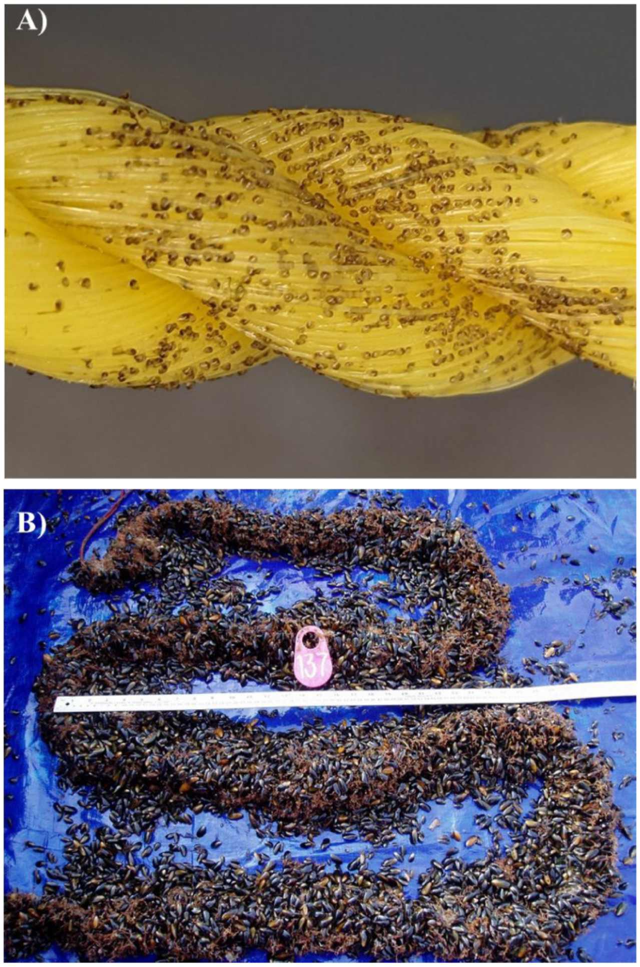
Key words: triploid mussels, suspension culture, byssogenesis, fall-off, performance, ecosystem services

Introduction

Mussels are key components of temperate rocky shore ecosystems, playing a vital ecological role (Smaal et al. 2019). Due to their rapid growth, high reproductive capacity, and strong adaptability, mussels are relatively easy to cultivate and represent a significant economic activity for coastal communities. Global aquaculture production of mussels reached approximately 1.9 million tons in 2022 (FAO 2024). With their rich nutritional profile, particularly by their high content of polyunsaturated fatty acids, they are considered as a valuable seafood commodity (Li et al. 2010). While cultivation methods have advanced in recent decades, mussel farming dates back to prehistoric time (Erlandson 1988). Mussel farming relies primarily on 3 genera (*Mytilus*, *Choromytilus*, and *Perna*) and 10 species: *Mytilus edulis* Linnaeus, 1758, *Mytilus trossulus* Gould, 1850, *Mytilus galloprovincialis* Lamarck, 1819, *Mytilus californianus* Conrad, 1837, *Mytilus platensis* A. d'Orbigny, 1846, *Mytilus planulatus* Lamarck, 1819; *Choromytilus chorus* (Molina, 1782); *Perna canaliculus* Philipsson, 1788, *Perna perna* Linnaeus, 1758, *Perna viridis* Philipsson, 1788 (Penney et al. 2008; Kamermans and Capelle 2019). In Canada, mussel production is a major sector within the bivalve aquaculture industry. In 2019, total Canadian mussel production reached 26 000 tons, valued at 43 million Canadian dollars. This accounted for 60% of the country's total bivalve production and 37% of the industry's revenue (Statistics-Canada 2019). Prince Edward Island is the primary production region, using *Mytilus edulis*, and contributing 80% of Canada's mussel yield. Mussel farming relies on the use of recently settled and metamorphosed juveniles, known as spat or seed. There are two main methods for obtaining mussel seeds: (1) collecting wild juveniles using artificial collectors, such as ropes, onto which mussels naturally attach (Fig. 1), and (2) hatchery production through controlled reproduction and larval rearing in a regulated environment (Kamermans and Capelle 2019). Wild seed collection is the more cost-effective approach; however, it is highly variable and unpredictable, with limited quality control and a high risk of biofouling (Mallet and Myrand 1995). In contrast, hatchery-based mussel production is more expensive but offers a stable and controlled supply of spat with selective breeding and triploid production possibilities enhancing their commercial value. However, hatchery operations and selective breeding strategies may affect the genetic variability of bivalves, with diminished genetic diversity potentially limiting the phenotypic plasticity and adaptability of cultured stocks (Nascimento-Schulze et al. 2021).

Once mussel seeds reach a shell length of approximately 20 mm, they are sorted by size and placed into mesh sleeves, also known as socks until they reach a marketable size (>55 mm) (Comeau et al. 2008). Although various mussel farming methods exist, longline culture is the only technique

Fig. 1. (A) Newly metamorphosed juvenile mussels attached to polypropylene rope. (B) Mussels larger than 20 mm attached to longline rope for sleeving.



used in eastern Canada. This method is well suited to the region's seasonal ice cover, as mussel sleeves are suspended a few meters below the water surface on floating longlines, reduces predation risks by keeping mussels off the seabed and ensures adequate food access for all individuals (Mallet and Myrand 1995). Longline farming supports the highest mussel growth rates compared to other methods, such as pole or on-bottom culture (Garen et al. 2004). However, this approach also presents challenges, including self-thinning and fall-off events (Fréchette 2012). Fall-off events have been reported in commercial mussel farms in several countries with studies linking them to weakened byssogenesis (Carrington 2002*b*; Lachance et al. 2008; Ni et al. 2024). In longline culture, mussel fall-off before harvest is significant, with reported losses ranging from 30% to 46% of total production (Bourque and Myrand 2006; Comeau et al. 2017). However, detachment from collectors is even more pronounced, with seed loss estimates between 75% and 89% (Comeau et al. 2015, 2017). An increase in population density may trigger self-thinning mechanisms, resulting in adverse effects on population dynamics due to heightened competition for space and resources, potentially culminating in elevated mortality rates.

Mussel fall-off shifts energy resources to the seabed, altering nutrient cycling and organic matter distribution (Fréchette 2012; Comeau et al. 2017). Fréchette (2012) estimated that the mussel biomass lost during the grow-out phase was nearly three times the biomass ultimately harvested and accounted for 59% of the total organic matter input to the seabed. Various environmental, biological, and handling factors contribute to mussel fall-off, from preseeding conditions to transport stress (South et al. 2021*a*, 2021*b*). Self-thinning and biofouling are major causes of the detachment, driven by competition for food and space (Fréchette et al. 1996, 2010; Guiñez 2005; Lachance-Bernard et al. 2010; Comeau et al. 2015, 2017; Gagnon 2019). Fall-off occurs when attachment strength is exceeded by external forces, which depend on factors such as byssal thread quality, the number of threads produced, attachment by neighbouring mussels, individual mussel mass, water velocity, wave action, and the angle of applied force relative to the byssal thread (Cole and Denny 2014; Carrington et al. 2015; Gagnon 2019). Detached mussels become a food source for benthic predators such as crustaceans, sea stars, and gastropods, leading to increased predator abundance near aquaculture sites (D'Amours et al. 2008; Wilding and Nickell 2013; Drouin et al. 2015; Sardenne et al. 2019). This predator aggregation can alter trophic interactions and community dynamics (Atalah et al. 2020; Brand and Jeffs 2022; Theuerkauf et al. 2022).

Attachment strength

Mussels attach to substrates, ropes, or other mussels using a specialized structure called the byssus. Byssal threads serve as critical attachment structures, allowing mussels to anchor themselves to various surfaces and withstand hydrodynamic forces such as waves and currents (Carrington 2002*a*). Thread diameter plays a key role in resistance and overall attachment strength. Analysis of the mechanical properties of byssal threads across various bivalve species found that diameter accounted for 62% of the ultimate force of the threads (Bouhlel et al. 2017). The quality and quantity of byssal threads are critical in determining attachment strength and are influenced by both abiotic and biotic factors. Environmental factors, including seawater temperature, pH, currents, food availability, noise, hypoxia, salinity, and pollutants, can significantly impact the production and mechanical properties of byssal threads (Fitzgerald-Dehoog et al. 2012; Babarro and Carrington 2013; Garner and Litvaitis 2013; Clements et al. 2018; Newcomb et al. 2019; Zhao et al. 2021; Ni et al. 2024). Influence of environmental conditions on byssal production and thread properties seem species-specific. High flow speeds can reduce thread performance of *Mytilus galloprovincialis*, making larger mussels more vulnerable to wave action in high-energy environments (Babarro and Carrington 2013). In contrast, studies on *Mytilus edulis* indicate that water flow and turbulence can stimulate byssal production, improving attachment strength (Lachance et al. 2008). Seasonal variations also affect byssal thread production and attachment strength, influenced by factors such as temperature, reproductive investment, and metal availability, which impacts the crosslinking between fibers (Lachance et al. 2008, 2011; Seguin-Heine et al. 2014). Experimental studies suggest that attachment strength and byssal production increase with rising water temperature up to an optimal threshold, beyond which byssal thread integrity is compromised, further weakening attachment (Moeser and Carrington 2006; Seguin-Heine et al. 2014).

The main documented biotic factors acting on byssogenesis of mussels are the development stages and the reproduction condition. In *Mytilus galloprovincialis*, larger mussels produce thicker but fewer byssal threads, suggesting a trade-off between thread quantity and mechanical quality (Babarro and Carrington 2013). After spawning, mussels invest less in byssogenesis due to the highly energetic cost of reproduction, increasing their risk of detachment from cultivation ropes (Babarro and Reiriz 2010; Hennebicq et al. 2013). In *Mytilus edulis*, spawning has been associated with a 32%–40% decline in byssal attachment strength (Lachance et al. 2008; Seguin-Heine et al. 2014), consistent with findings in *Mytilus galloprovincialis*, where post-spawning mussels exhibit reduced byssogenesis and lower food absorption efficiency (Babarro and Reiriz 2010). Spawning results in thinner byssal threads with lower amino acid concentrations, particularly histidine and lysine, weakening attachment strength (Hennebicq et al. 2013). Gametogenesis is highly energy-intensive, accounting for around 50% of the mussel's total energy expenditure (Lachance et al. 2008; Babarro and Reiriz 2010). Meanwhile, byssogenesis itself demands 8%–15% of the mussel's energetic budget (Babarro and Reiriz 2010) and this demand can rise to as much as 47% in individuals stimulated to produce byssal threads daily (Roberts et al. 2021). This highlight the crucial role of energy allocation in mussels and emphasize the energetic trade-offs mussels encounter, particularly in turbulent environments, where energy is redirected toward protective structures such as byssal threads and increased shell thickness, often at the cost of reproductive tissues (Carrington 2002*a*, 2002*b*; Moeser and Carrington 2006; Lachance et al. 2008, 2011; Babarro and Carrington 2013). By synthesizing research on mussel byssogenesis, a clearer understanding of the multifactorial influences on byssal thread secretion and quality can be achieved. This knowledge is essential for improving local mussel production, particularly in developing strategies to enhance byssal attachment and reduce fall-off rates in suspension-cultured systems.

Mussel ecosystemic services

Human activities, such as agriculture and aquaculture requiring feed inputs for fish and crustaceans, can lead to the release of significant amounts of nutrients into the environment, particularly nitrogen and phosphorus (de Lacerda et al. 2006). These authors documented substantial nitrogen and phosphorus inputs across six Brazilian estuaries, where anthropogenic emissions were one to two orders of magnitude higher than natural emissions. Their study identified shrimp farms as the primary source of nitrogen (1.9 t km^{-2} year^{-1}), followed by crop agriculture (1.3 t km^{-2} year^{-1}) and livestock farming (0.7 t km^{-2} year^{-1}). In contrast, the largest contributors to phosphorus emissions were livestock farming (0.9 t km^{-2} year^{-1}) and crop agriculture (0.34 t km^{-2} year^{-1}), while shrimp farms accounted for 0.23 t km^{-2} year^{-1}. Excess nitrogen and phosphorus inputs stimulate phytoplankton production, potentially leading to eutrophication (Diaz and Rosenberg 2008). One of the most severe consequences of eutrophication is the depletion of dissolved oxygen (DO), creating hypoxic zones when DO concentrations fall below 2 mL O_2 L^{-1} (Diaz and Rosenberg 2008). The decline in DO is partially driven by phytoplankton respiration at night (Burkholder and Shumway 2011), but primarily results from microbial activity breaking down dead phytoplankton (Wallace et al. 2014). Additionally, transient hypoxic events can be exacerbated by mass mortality events in benthic fauna, which further increase organic matter inputs and fuel microbial growth (Diaz and Rosenberg 2008).

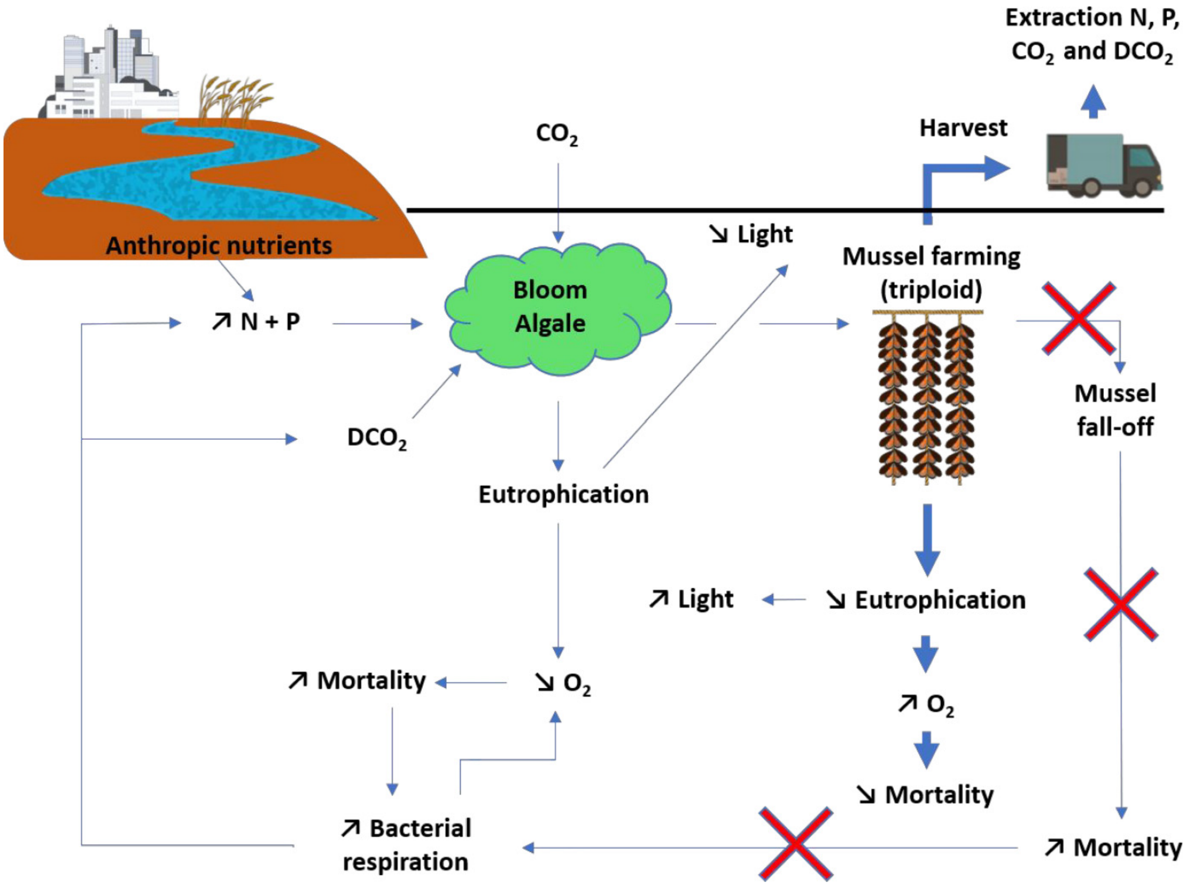
Bivalve farming is widely regarded as one of the most environmentally sustainable aquaculture practices, as it requires no external feed (Garlock et al. 2020; Suplicy 2020). Furthermore, this food production is considered as a form of extractive aquaculture that provides ecosystem services by capturing excess nutrients and converting them into bivalve biomass (Lindahl et al. 2005; Naylor et al. 2021; Cubillo et al. 2023). Mussels, in particular, possess a strong filtration capacity, efficiently clearing water of organic particles, even at low temperatures (Cusson et al. 2005). This enables them to consume large quantities of nutrient-rich phytoplankton, thereby mitigating the impacts of eutrophication (Cubillo et al. 2023). Studies on *Mytilus edulis* have demonstrated that eutrophic environments with high phytoplankton concentrations promote rapid mussel growth. A review analyzing 62 bivalve farming ecosystems found that only 4 had significant adverse environmental impacts, primarily in poorly flushed lagoons with high bivalve biomass (Burkholder and Shumway 2011). Suspended culture methods optimize mussel distribution throughout the water column, significantly increasing both the number of farmed bivalves and the overall clearance rate per unit of surface area compared to benthic populations. Research has quantified these filtration benefits and 13%–31% reduction in particle concentrations were observed inside a mussel farm (Nielsen et al. 2016) and chlorophyll-a (Chl-a) depletion of up to 69% was reported in another mussel farms (Taylor et al. 2021). The use of a coupled hydro-biogeochemical model to examine the interactive effects of various factors (bay geomorphology, nutrient discharges, bivalve species, farmed bivalve area, water temperature, sea level, and precipitation) on the degree of estuarine nutrient mitigation by farmed bivalves indicated a net nitrogen removal in the majority of the tested model scenarios (Guyondet et al. 2022). Mussels also contribute to nutrient removal through their byssal threads, which can incorporate up to 21% nitrogen (Hawkins and Bayne 1985). Petersen et al. (2014) estimated that 11%–19% of nitrogen removal from Skive Fjord (Denmark) via blue mussel harvesting was attributable to byssal thread production. Thus, the ability of bivalves to graze on phytoplankton has been shown to provide numerous ecological services, including improved water clarity, enhanced seagrass health, suppression of toxic algal

Fig. 2. The hydrodynamic flume was used to characterize byssogenesis under standardized laboratory conditions, with a phytoplankton ration equivalent to 5% of mussel dry mass, a salinity of 27, a temperature of 18 °C, and a unidirectional current velocity maintained for 72 h.

blooms, reduction of microbial pathogens, and sequestration of biotoxins and contaminants (Smaal et al. 2019).

As bivalves do not require feed inputs, they are attractive candidates for the expansion of sustainable seafood, as argued for more than 30 years (Naylor et al. 2021). In addition to their nutrient extraction capacity, bivalves are the blue food group with the lowest CO_2 emissions, lower than their capture counterparts with 1414 versus 11 400 kg CO_2 equivalent per tonne (Gephart et al. 2021). CO_2 is emitted during shell formation (Ray et al. 2018) and transport (Iribarren et al. 2010). Mussel farming has a relatively low carbon footprint since it involves minimal boat and engine use, with the main environmental impact stemming from fuel consumption for transportation of mussels from farms to market (Aubin et al. 2018). Furthermore, bivalves are among one of the highest-quality nutritional products across all types of aquatic foods (Golden et al. 2021). Some recent study suggests that bivalve culture could be considered as a carbon sink, until an average of 55 t of carbon sequestrated per farm (0.25 ha) over a cultivation cycle of 17 months (Vaher et al. 2024). However, because the carbon sequestered in mussel shells originates mainly from (bi)carbonate ions, current evidence does not support the idea that mussel farming plays a role in net CO_2 capture or climate mitigation (Pernet et al. 2025). Furthermore, the use of models estimated that stored oceanic carbon by bivalve aquaculture was equivalent to 0.001% of Canadian anthropogenic CO_2 emissions (Zavell et al. 2023). Thus, bivalve farms may not solve climate change, but they provide a protein source with the lowest CO_2 emissions.

Fig. 3. Illustration of the potential ecological benefits of triploid mussels in reducing eutrophication. Bold arrows indicate enhanced effects attributed to triploid mussels, while red crosses denote the reduction or inhibition of specific processes due to their triploid nature.

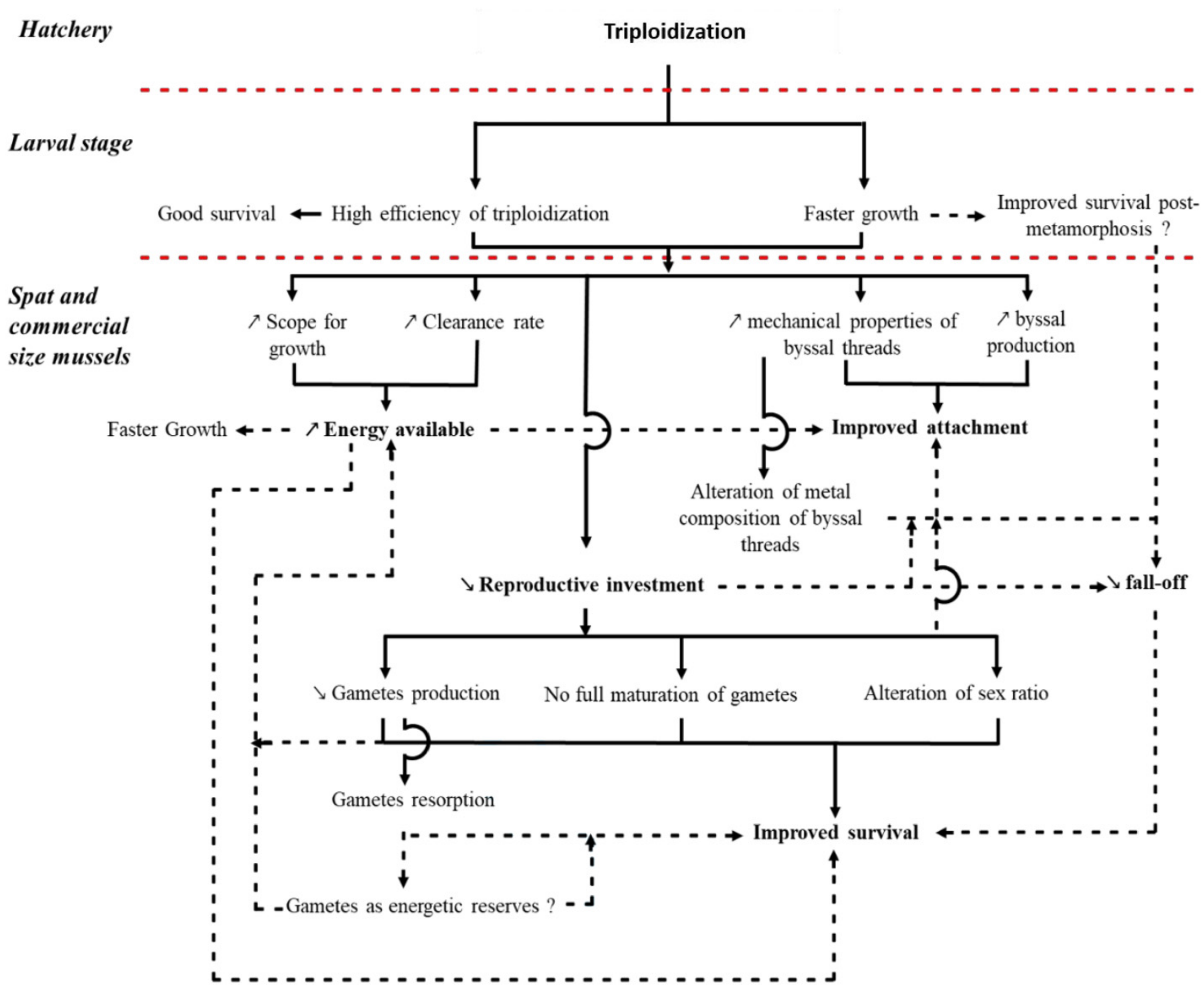


However, mussel fall-off can diminish these environmental benefits. Fallen mussels are consumed by predators and microbial organisms, leading to nutrient re-release into the seawater, which can exacerbate eutrophication. The breakdown of dead mussels also increases oxygen consumption and CO_2 emissions due to bacterial respiration. Furthermore, over time, the dissolution of $CaCO_3$ in decomposing shells may return sequestered carbon to the environment unless the shells are buried under sediments.

Polyploidy

Fish and bivalves are naturally diploid, meaning their DNA is organized into pairs of chromosomes. However, it is possible to intervene during fertilization to introduce an additional set of chromosomes, resulting in triploid organisms. Triploid fish, such as trout and salmon, and triploid bivalves, including oysters, clams, mussels, and scallops, exhibit reduced fertility or, in some cases, complete sterility (Allen et al. 1982, 2021; Brake et al. 2002; Benfey 2016; Osterheld et al. 2021; Jiang et al. 2024). The reduced fertility observed in triploid bivalves is often linked to lower reproductive investment, with energy being redirected toward other physiological and metabolic processes, such as growth (Ruiz-Verdugo et al. 2000; Osterheld et al. 2024). Multiple studies have shown that triploid bivalves exhibit faster growth rates (Allen Jr. and Downing 1990; Brake et al. 2004; Osterheld et al. 2023; Vignier et al. 2025). Triploid mussels exhibit higher clearance rates (food ingestion), which enhance growth (Osterheld et al. 2023). Combined with reduced energy investment in reproduction, this allows for resource reallocation toward tissue, shell, and byssal thread production (Osterheld et al. 2024). In laboratory standard conditions, triploid mussels produced up to 65% more threads than the diploids produced by the same parents with enhanced mechanical properties, including 45% greater stiffness and increased resistance to deformation (Fig. 2; Osterheld et al. 2023). Triploid mussels resorb their gametes, potentially recovering some of the energy invested in reproduction. This could serve as an energy reserve during the reproductive season, allowing triploid mussels to maintain better condition than diploids. As a result, triploids may experience less post-spawning weakening, reduced fall-off and increased ecosystem services (Fig. 3; Osterheld et al. 2024). Additionally, this energy reallocation may enhance immunity, providing triploids with greater resistance to pathogens (Nell 2002; Duchemin et al. 2007; Brianik and Allan 2023). In oysters, for example, triploids have demonstrated higher phagocytic activity, leading to increased tolerance to harmful algal toxins, such as those produced by *Alexandrium minutum* Halim, 1960 (Haberkorn et al.

Fig. 4. A summarized representation of the potential impacts of triploidy on mussel production. Solid black arrows indicate direct links supported by literature (Brake et al. 2004; Osterheld et al. 2021, 2023, 2024), while dotted black arrows represent hypothetical connections. Red dotted lines distinguish the different stages of mussel development.



2010). However, these findings remain subject to debate, as several studies have reported that triploidy offers neither a clear advantage nor a disadvantage in oysters in terms of disease resistance (Dégremont et al. 2015; Brianik and Allan 2023). Nonetheless, due to their faster growth, triploids have a shorter exposure period to disease. The advantages of triploidy appear to be influenced by environmental conditions (Brake et al. 2004; Duchemin et al. 2007). In oysters, triploidy has been associated with enhanced growth in warmer climates, suggesting that temperature plays a significant role in determining its benefits (Nell 2002). Similarly, in lion scallops, food availability influenced the triploid advantage, as in nutrient-rich environments, the reliance on energetic reserves decreased, reducing the differences between diploid and triploid individuals (Racotta et al. 2008).

Conclusion

Triploid mussels offer clear advantages for mussel farmers and coastal ecosystems by promoting enhanced growth, stronger attachment, and reduced reproductive investment, which could improve ecosystem services (Fig. 4). Their lack of a reproductive season enables year-round commercialization with consistent meat quality, making them a valuable product for commercial markets. Economically, triploid mussels could reduce operational costs for mussel farmers. Their lower fall-off rates minimize handling requirements, decreasing the number of boat trips needed for maintenance, which in turn reduces fuel consumption and emissions. Additionally, their ability to thrive at lower density reduces self-thinning and manual density adjustments, further lowering labor and fuel costs. Their stronger attachment and reduced loss rates on longlines also enhance growth efficiency and reduce the need for frequent interventions. These factors contribute to lower production expenses and higher revenue potential for farmers. Beyond economic benefits, triploid mussels present significant environmental advantages. Their superior attachment and ability to grow efficiently at lower density support greater nutrient removal and carbon sequestration, enhancing the sustainability of mussel farming. As effective extractive species, they may help control eutrophication and even mitigate climate change impacts. Additionally, triploid mussel farming could represent a highly sustainable aquaculture practice with a low to potentially negative carbon footprint. Overall, triploid mussels hold great promise for advancing both economic viability and environmental sustainability in mussel aquaculture. Further research is necessary to optimize their commercial integration and assess their long-term ecological impacts. As the most widely applied form of genetic manipulation in the global oyster aquaculture industry, triploidy is extensively adopted by producers in several countries, indicating a degree of public acceptance (Kiffney et al. 2025). Nonetheless, the scientific community must take a proactive stance in advancing research on regulatory frameworks and public perception to ensure responsible and transparent deployment in mussels' industry.

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