



REVIEW

Status of Red Swamp Crayfish Aquaculture and Genetic Improvement in China

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Received: 27 May 2025 | **Revised:** 16 August 2025 | **Accepted:** 22 August 2025

Funding: This work was supported by Temasek Life Sciences Laboratory, Singapore.

Keywords: aquaculture | concern | crayfish | development | genetic improvement | sustainability

ABSTRACT

China is the world's leading producer of red swamp crayfish (*Procambarus clarkii*). The aquaculture of *P. clarkii* and its related industry generated annual value over 458 billion Chinese yuan in 2022, contributing significantly to food security, livelihoods, and economic development. This review analyzes the status of the industry, highlighting its biological characteristics, farming practices, economic importance, and challenges. *P. clarkii* is adaptable and reproduces rapidly, but it is also invasive and disrupts native species diversity. Environmental concerns include water quality degradation and habitat loss. Disease outbreaks and regulatory issues pose additional challenges. Research is ongoing to improve broodstocks, seed production efficiency, and sustainability through breeding programs, better management practices, and technologies. China's crayfish aquaculture can achieve long-term growth and contribute to a sustainable future. This can be done by overcoming challenges and embracing key innovations. These include selective breeding, genomic selection, monosex production, genome editing technologies, and improved production systems.

1 | Introduction

The red swamp crayfish (*Procambarus clarkii*) is a freshwater crustacean species native to North America, known for its adaptability and rapid reproductive rate [1]. Currently, *P. clarkii* is present in over 40 countries on four continents, and there is still potential for further expansion [2, 3]. Introduced to China in the 1920s [4], it has since become a prominent species in Chinese freshwater aquaculture systems recently [5]. Its annual aquaculture production in China is over 2.39 million metric tons in 2020 [5]. With its robust growth characteristics and high market demand, the red swamp crayfish has established itself as a valuable commodity in both domestic and international markets [5, 6].

Crayfish aquaculture plays a significant role in China's aquaculture sector, contributing to food security, rural livelihoods, and economic development [5, 6]. *P. clarkii*, in particular, has emerged as a key species within this industry due to its high reproductive potential, adaptability to various environmental conditions, and consumer preference for its meat [6]. *P. clarkii* farming provides employment opportunities for rural communities and serves as an important source of income for farmers, especially in regions where alternative livelihood options may be limited. Since its aquaculture in the 1980s, extensive research on the biology, reproduction [7], diseases [8–10], genetics [4, 11], genomics [12, 13] and aquaculture technologies [14, 15] of *P. clarkii* has been conducted in China, leading to numerous breakthroughs. However, most papers on *P. clarkii* biology and

aquaculture were published in Chinese journals; it is hard for scientists outside China to get updated information. In addition, since a review of crayfish aquaculture in China published in 2018 [5], no updates on the status of crayfish aquaculture in China have been published.

This review paper aims to provide a comprehensive overview of the status of *P. clarkii* aquaculture and research in China. By synthesizing existing literature and research findings, we explore various aspects of crayfish aquaculture, including its biological characteristics, aquaculture practices, geographical distribution, economic significance, challenges, and prospects. Through this analysis, we seek to enhance understanding of the dynamics shaping the crayfish aquaculture industry in China and identify key areas for further research priorities. Ultimately, this review aims to contribute to the sustainable growth and management of red swamp crayfish aquaculture in China and beyond.

2 | Biology and Ecology of *P. clarkii*

P. clarkii exhibits distinct morphological characteristics that aid in its identification [16] (Figure 1A,B). Typically, adults range from dark red to olive green in color, with a prominent pair of pincers and a segmented body covered in a hard exoskeleton [2]. They possess five pairs of walking legs and a pair of specialized appendages, called swimmerets, which aid in reproduction. Swimmerets serve distinct reproductive functions in males and females [16]. In males, the first two pairs of swimmerets are modified into hardened, rod-like

structures called gonopods, which are used to transfer spermatophores to the female during mating, while the remaining swimmerets may aid in holding the female during copulation. In contrast, females possess soft, feathery swimmerets that are used to carry and aerate fertilized eggs. After mating, eggs are attached to the swimmerets, where they remain until hatching. The swimmerets help circulate water around the eggs, providing oxygen and removing waste to support embryonic development [16]. The life cycle of red swamp crayfish comprises several stages, starting with egg deposition, followed by hatching into larvae, development into juveniles, and eventual maturation into adults [17]. The duration of each stage varies depending on environmental conditions such as temperature and food availability [18] (Figure 1C). *P. clarkii* is highly adaptable to various aquatic habitats, including freshwater ponds, lakes, rivers, and wetlands [19]. They prefer shallow and slow-moving waters with abundant vegetation and organic matter, which provide cover and food sources [1]. Optimal habitat conditions for crayfish include moderate water temperatures ranging from 20°C to 30°C, dissolved oxygen levels above 4 mg/L, and pH levels between 6.5 and 8.5 [5]. *P. clarkii* is sensitive to changes in water quality and habitat degradation, making proper management essential for successful aquaculture [5].

Reproductive biology plays a crucial role in the life cycle of *P. clarkii* and influences population dynamics in aquaculture settings [20, 21]. *P. clarkii* reaches sexual maturity at the age of 3 to 6 months depending on culture conditions [22]. *P. clarkii* reproduction is characterized by direct sperm transfer from males to

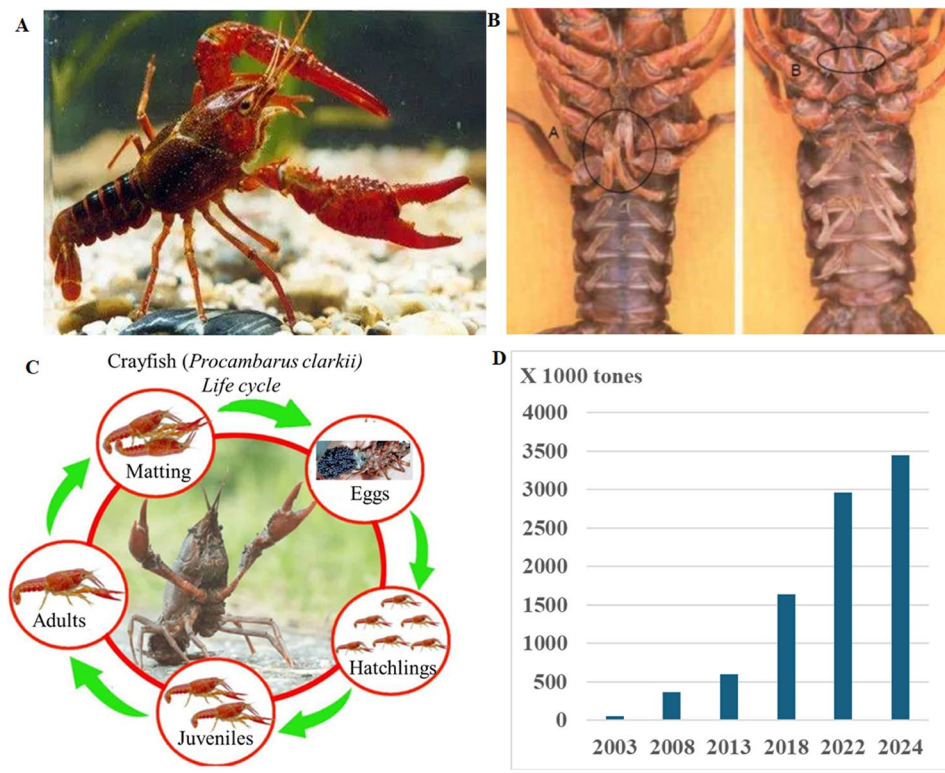


FIGURE 1 | Red swamp crayfish (*Procambarus clarkii*) and its annual aquaculture production in China. (A) Adult red swamp crayfish. (B) Male (left) and female (right) show difference in reproductive structures (gonopods and gonopores). (C) Life cycle of red swamp crayfish usually spans about 1 year, but this can vary depending on environmental conditions such as temperature, food availability, and habitat quality. (D) Annual red swamp crayfish aquaculture production in China in 2003, 2008, 2013, 2018, 2022, and 2024.

females through specialized structures called gonopods during mating (Figure 1C). Females carry fertilized eggs on their abdomen until hatching, after which they release larvae into the water [20, 21]. *P. clarkii* exhibits high reproductive potential, with females capable of producing multiple broods (300 to over 1000 eggs) per year under favorable conditions [21, 23]. However, reproduction may be influenced by factors such as temperature, photoperiod, and nutritional status [24, 25].

In aquaculture settings, *P. clarkii* displays various behaviors related to feeding, mating, and territoriality [26–28]. It is an opportunistic omnivore, scavenging on detritus, algae, aquatic plants, and small invertebrates [29]. *P. clarkii* also engages in social interactions, including agonistic behaviors such as aggression and dominance hierarchy establishment. Understanding *P. clarkii* behavior is essential for optimizing feeding strategies, preventing cannibalism, and managing stocking densities in aquaculture ponds [29]. Additionally, crayfish play a role in ecosystem dynamics by influencing nutrient cycling, benthic habitat structure, and prey populations within aquatic ecosystems [24].

3 | Status of Aquaculture Production of *P. clarkii* in China

3.1 | Historical Perspective

The introduction of *P. clarkii* to China can be traced back to the 1920s [4]. The first known introduction of *P. clarkii* occurred in Nanjing, Jiangsu Province, marking the beginning of its aquaculture in China.

The study on *P. clarkii* biology in China started much later than other countries, including the USA [16]. In China, early efforts

in crayfish aquaculture focused on understanding the species' growth [30, 31], reproduction [32, 33], diseases [34], genes related to disease resistance [35], genetics [4, 36, 37], and optimal farming practices [38]. Experimental trials were conducted to assess the feasibility of crayfish farming in different regions of China, with initial successes recorded in areas with suitable freshwater habitats and mild climatic conditions [38]. Techniques for pond culture, rice field culture, and indoor farming, feeding, and disease management were gradually refined, paving the way for larger-scale production [6, 38].

The *P. clarkii* aquaculture industry in China experienced significant growth and expansion in the latter half of the 20th century and into the 21st century (Figure 1). As demand for crayfish for food increased both domestically and internationally, farmers across various regions of China began to intensify production and adopt more efficient farming practices (Figures 2 and 3). Technological advancements, such as improved breeding techniques [39], feed formulations [40], culture systems [38] and disease management strategies [41], contributed to increased productivity and profitability [6]. By the late 20th century, crayfish farming had become a widespread and lucrative industry in China, with production volumes rising steadily each year [5, 6]. Government support and favorable policies further incentivized the expansion of crayfish aquaculture, leading to the establishment of specialized hatcheries, research institutes, and extension services dedicated to supporting the sector [5]. China stood as the world's leading producer of crayfish, with 2.96 and 3.45 million metric tons harvested annually in 2022 and 2024 (Figure 1D) [6, 42].

3.2 | Aquaculture Practices of *P. clarkii* in China

Successful *P. clarkii* aquaculture begins with the careful selection and management of broodstock [5]. Broodstock is selected based



FIGURE 2 | Seed production, transport, and release of red swamp crayfish for aquaculture in China. (A) Crayfish hatchery for seed production and aquaculture in rice fields. (B) Indoor production of juvenile red swamp crayfish in tanks. (C) Juveniles prepared for transport to farms. (D): Air-conditioned vehicle used for transporting juveniles to farms. (E) Releasing juveniles into ponds or rice fields for production. (F) Rice fields utilized for crayfish production.

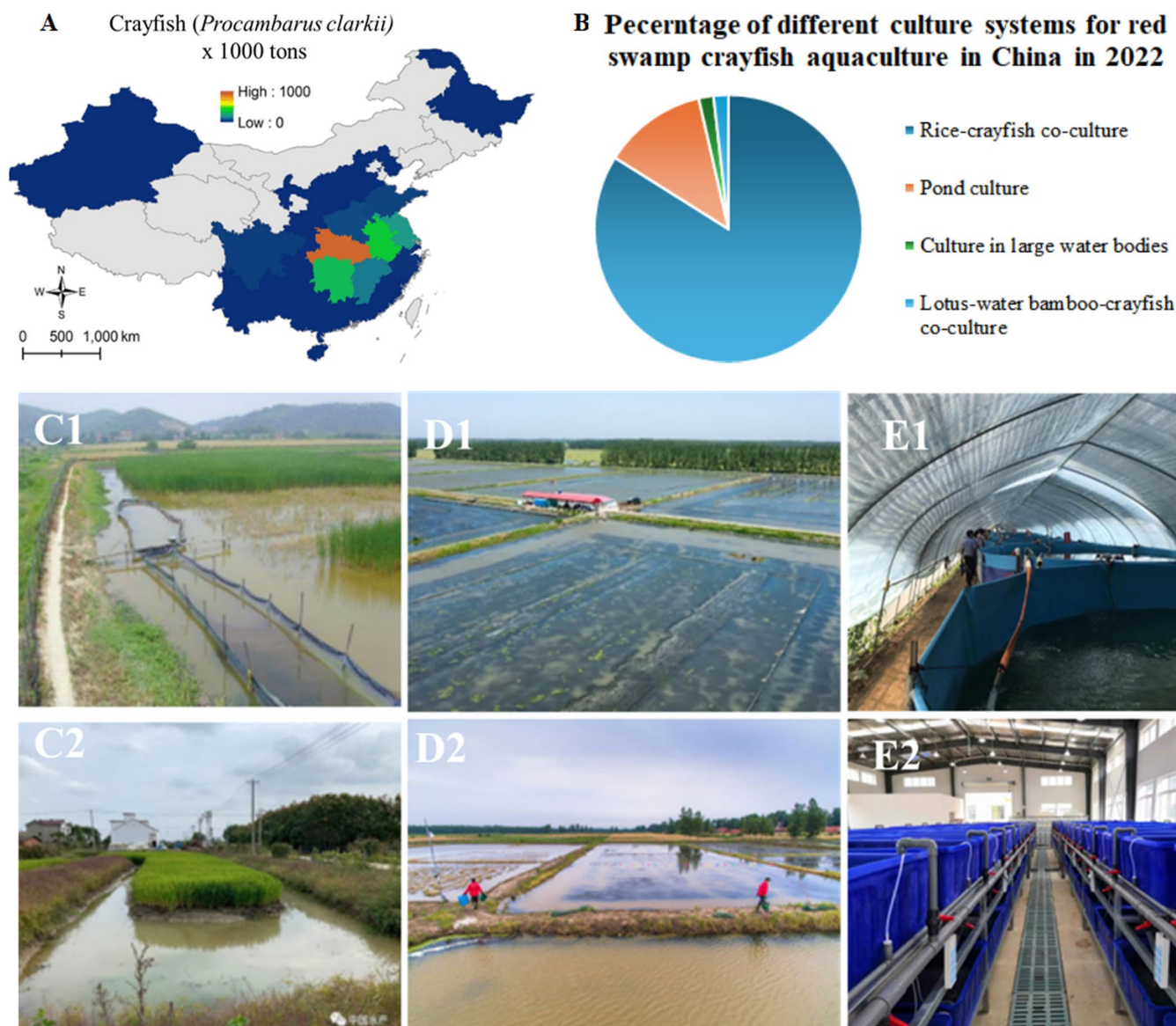


FIGURE 3 | Distribution and aquaculture systems of red swamp crayfish in China. (A) Map showing the primary locations of red swamp crayfish aquaculture in China. (B) Distribution of different culture systems used for farming red swamp crayfish. (C1 and C2) Rice-fish-crayfish integrated culture system. (D1 and D2) Rice fields and ponds dedicated to crayfish culture. (E1 and E2) Indoor tank farming of crayfish under controlled conditions, including lighting, temperature, dissolved oxygen levels, and feeding schedules.

on criteria such as size, weight, reproductive performance, and genetic diversity to ensure the production of healthy offspring with desirable traits. The seed supply method for Chinese crayfish production involves multiple linked steps, including seed production, transportation, and supply [5]. For seed production, there are generally two approaches: natural production/semi-artificial breeding and controlled breeding [5, 6]. In natural reproduction, *P. clarkii* reproduces in a natural state through mating and spawning. Farmers can rely on the mature crayfish in the breeding pond to breed themselves naturally, solving the problem of seed supply and saving breeding costs [5, 43]. However, this method has problems such as difficulty in controlling the breeding time, uneven sizes of offspring, and difficulty in collection. In semi-artificial breeding, improvement of the quality and quantity of seedlings can be achieved through human intervention, such as selecting excellent parents, controlling the breeding environment, and increasing breeding

facilities [43–47]. For example, a special breeding tank should be established to select large and robust broodstock for centralized breeding. Full controlled breeding is an efficient and controllable method of seed production (Figure 2A,B). By establishing indoor cement pools and other facilities, and using flowing water or aeration combined with regular water changes, we can provide a good environment for the growth and development of crayfish seedlings [48, 49]. This method can achieve high-density nursery and provide sufficient seedlings at regular intervals, thereby greatly increasing crayfish production [50]. Factory nursery facilities include indoor hatching tanks, nursery tanks, water supply systems, gas supply systems, and power supply equipment. At the same time, special aquaculture paint needs to be painted on the nursery ponds, breeding ponds, and breeding ponds to isolate the contact between the water and the pond, avoid the precipitation of harmful substances, and ensure the survival rate of seedlings [43, 48, 50, 51].

China is a vast country, therefore, to ensure seed survival to reach the culture sites, transportation methods are critically important [52]. There are several approaches, including dry transportation and transport with water and oxygenation [52]. Dry transportation uses reinforced mesh boxes, plastic boxes, or foam boxes for transportation (Figure 2C,D), which is subdivided into water spray transportation by cold fresh trucks and aircraft air transportation [52, 53]. This method is suitable for the transportation of juvenile crayfish weighing approximately 5 to 7 g over short or medium distances, up to 300 km. Transport with water and oxygenation typically uses double-layer nylon bags filled with oxygen to transport crayfish seeds. Transport with water and oxygenation typically uses double-layer nylon bags filled with oxygen to transport fry [48, 49]. This is suitable for the long-distance transportation of newly hatched larvae, which weigh approximately 0.016 to 0.025 g, and can ensure the survival rate of fry during transportation. The survival rate of crayfish seedlings transported over short distances (3 to 5 h) is over 80%, and there are also successful examples of long-distance transport (5 to 40 h) [48, 49]. This is due to the continuous improvement of transportation methods and the improvement of transportation technology. The comparative advantages and disadvantages of these transport methods are listed in Table S1.

P. clarkii seeds mainly come from professional breeding bases, farms, or fishery cooperatives. These units usually have complete breeding facilities and rich breeding experience and can provide high-quality seedlings [5, 43, 44, 46, 50]. At the same time, with the continuous development of the crayfish farming industry, more and more companies and individuals have begun to get involved in the field of seed breeding [54], providing the market with more supply options. April to June every year is the peak season for seed supply [43–45, 48, 51]. This is the time for transplanting rice seedlings and slowing down seedlings, so it is suitable for culturing seedlings. In addition, the price of crayfish seeds in June is relatively low, making it suitable for breeding investment [55]. Farmers can learn about the supply of crayfish seedlings through local fishery departments, aquatic products markets, or fishery cooperatives, and choose appropriate suppliers for purchase [5]. When purchasing crayfish seedlings, make sure they are fresh and healthy, and understand the supplier's supply channels and legality to ensure the quality and reliable source of the seedlings. In summary, the seed supply methods for *P. clarkii* production in China include natural breeding, semi-artificial breeding, factory breeding, and various transportation methods. Together, these methods constitute a complete chain of crayfish seed supplies, providing a strong guarantee for the development of the crayfish farming industry.

Aquaculture systems for *P. clarkii* in China have evolved into sophisticated and efficient operations tailored to meet the growing market demand [5, 6, 56]. These systems vary in scale, from small-scale backyard ponds to large-scale commercial farms utilizing advanced technologies (Figures 2 and 3). At present, the most common crayfish farming model in China is rice-crayfish integrated farming (rice-crayfish rotation), which accounts for more than 80% of the total crayfish farming area [56, 57]. These rice-crayfish integrated farming areas can range in size from a few hundred square meters to several hectares. Ponds are designed to hold a certain density (45,000 to 90,000 individuals

per hectare) of crayfish, with water quality carefully managed through regular water exchange, aeration, and fertilization. Natural and formulated feeds are provided to support crayfish growth. Another innovative aquaculture system is the rice-crayfish integrated system [38, 56], where crayfish are reared in rice paddies. This system leverages the mutual benefits of rice cultivation and crayfish aquaculture. Crayfish feed on pests and weeds in the rice paddies, reducing the need for chemical pesticides and fertilizers. In turn, the rice provides shade and habitat for crayfish, while the organic matter from rice roots and residues enriches the water, promoting crayfish growth [58]. Under optimal conditions, yields of 1125 to 2250 kg/ha/year can be achieved, especially when integrated with rice (e.g., rice-crayfish systems) or monoculture in purpose-built ponds [58]. While not as widespread as pond-based or rice-crayfish systems, some commercial farms in China are experimenting with recirculating aquaculture systems (RAS) for *P. clarkii* [48, 50]. RAS allows for greater control over water quality and waste management, reducing the environmental impact of aquaculture. Water is continuously filtered, oxygenated, and recirculated within the system, with minimal water exchange required. This system is particularly suitable for high-density, indoor aquaculture operations [50, 51]. Aquaculture systems for red swamp crayfish in China are closely tied to market demand [47, 48, 51]. Farmers carefully manage their production cycles to coincide with peak market seasons, ensuring a steady supply of crayfish for consumers.

P. clarkii require a balanced diet to support growth, reproduction, and overall health [24]. Feed formulations typically include protein-rich ingredients such as fishmeal, soybean meal, and cereal grains, supplemented with vitamins, minerals, and lipids [59, 60]. Feeding strategies may vary depending on crayfish life stage, pond conditions, and seasonal changes in nutrient availability [61, 62]. Proper feeding management is essential to prevent nutrient waste, water quality degradation, and overfeeding-related issues. The commercial feeds for crayfish aquaculture in China are currently witnessing a growing demand driven by the expanding crayfish farming industry [5, 6, 63]. Manufacturers (e.g., Huai'an Kangda Feedstuff Limited Company: www.jskdjt.com) are developing specialized feeds tailored to the nutritional requirements of different crayfish species, considering their growth stages and environmental conditions. These feeds are formulated with high-quality ingredients to ensure optimal growth, health, and coloration of crayfish. As the industry matures, there is a trend toward increased research and development to improve feed efficiency and reduce environmental impact [61]. However, the market is still relatively fragmented, with a variety of brands and formulations available. Additionally, fluctuations in raw material prices and supply chain disruptions can impact the availability and cost of commercial crayfish feeds. Overall, the commercial feeds sector for crayfish aquaculture in China is dynamic and evolving, with ongoing efforts to meet the growing needs of the industry while also ensuring sustainability and profitability.

Maintaining optimal water quality is essential for crayfish health and productivity in aquaculture systems [24]. Key parameters such as dissolved oxygen (4–6 mg/L), pH (6.5–8.5), temperature (20°C–30°C), ammonia (<0.05 mg/L), nitrite (<0.1 mg/L), and nitrate (<50 mg/L) levels are regularly monitored and managed

to ensure a suitable environment for crayfish growth and survival [64]. Water quality management practices may include aeration, water exchange, nutrient management, and pollution control measures to minimize stress and disease susceptibility. Disease outbreaks can have devastating effects on crayfish aquaculture operations, leading to production losses and economic damages [41]. There are many diseases caused by pathogens, including white spot syndrome virus (WSSV), *Aeromonas hydrophila*, *Vibrio* spp., *Pseudomonas* spp., *Aphanomyces astaci*, *Microsporidia*, *Branchiobdellids*, and *Haplosporidium* spp. [65–68]. For instance, the outbreak of white spot syndrome virus (WSSV) in crayfish farms has led to massive mortality rates, decimating entire stocks and disrupting supply chains. This not only results in direct financial losses for farmers but also impacts the wider industry, including processors, distributors, and retailers [69, 70]. Another example is the spread of bacterial infections such as vibriosis, which can rapidly spread through crayfish populations, causing severe illness and mortality [71, 72]. These outbreaks require immediate intervention, including the use of antibiotics and quarantine measures, which can be costly and time-consuming. The economic impact of such diseases can be severe, with farmers facing significant financial burdens and the potential for long-term damage to their operations [41]. Disease prevention strategies focus on biosecurity measures, including quarantine protocols, pathogen screening, and farm hygiene practices to minimize the introduction and spread of pathogens [73, 74]. Disease control measures may involve the use of probiotics, immunostimulants, and antimicrobial agents under veterinary supervision to mitigate disease impacts and maintain crayfish health.

3.3 | Geographical Distribution of *P. clarkii* Farms in China

3.3.1 | Overview of Major *P. clarkii*-Producing Regions

P. clarkii farming in China is distributed across over 20 provinces, with certain areas emerging as major production hubs. Provinces such as Hubei, Hunan, Jiangsu, and Anhui are among the leading crayfish-producing regions (Figure 3A) [5, 56]. This might be because *P. clarkii* was first introduced to these provinces [4]. Moreover, these regions offer favorable environmental conditions, such as abundant freshwater resources, a suitable climate, and ample land availability, which support large-scale crayfish farming operations [5, 56]. Additionally, proximity to markets and transportation networks enhances the competitiveness of these regions in crayfish production [56].

3.3.2 | Regional Differences in Production Practices and Challenges

Despite the widespread distribution of *P. clarkii* farms across different regions, there are notable variations in production practices and challenges [6, 50, 56, 58]. In some regions (such as in Anhui and Hubei provinces), traditional extensive farming methods prevail, characterized by low-input, low-intensity production systems primarily reliant on natural pond ecosystems [75]. In contrast, regions like Jiangsu Province have a crayfish industry characterized by more diverse production methods, a longer history of development, and higher investment in breeding. In addition to rice

and crayfish farming, Jiangsu's crayfish and crab, lotus root and crayfish, and other models are also very distinctive. The crayfish produced in Jiangsu are larger in size and better in quality [76]. In addition to the traditional Yangtze River Basin and Huaihe River Basin, Hainan and Northeast China are now attracting more and more attention for crayfish farming, and the production area is gradually increasing [5, 6]. Regional challenges may include fluctuations in market demand, regulatory constraints, and environmental pressures, which influence the adoption of specific production models and management strategies [6].

3.3.3 | Environmental Impacts and Sustainability Considerations

The expansion of crayfish farming in China has raised concerns about its potential environmental impacts and long-term sustainability [56, 77]. Intensive farming practices, such as high stocking densities and use of fertilizers and feed additives, can lead to water pollution, habitat degradation, and ecosystem disturbances [5]. Additionally, habitat conversion for pond construction and water resource depletion may exacerbate environmental pressures in certain regions [5, 6]. To address these challenges, efforts are underway to promote sustainable crayfish farming practices, including water resource management, habitat restoration, and adoption of eco-friendly production technologies [5, 6]. Sustainable certification schemes and environmental regulations could play a crucial role in promoting responsible aquaculture practices and mitigating environmental risks associated with crayfish farming.

3.4 | Economic Impact and Market Trends

3.4.1 | Contribution of *P. clarkii* Aquaculture to the Chinese Economy

P. clarkii aquaculture plays a significant role in the Chinese economy, contributing to employment, income generation, and rural development. According to estimates [6], the comprehensive revenue of the China crayfish industry in 2022 is 458 billion Chinese yuan. Among them, the revenue from the primary industry is 96 billion Chinese yuan, accounting for 20.96%; the revenue from the secondary industry is 49.8 billion yuan, accounting for 10.87%; the output value of the tertiary industry is 312.2 billion yuan, accounting for 68.17% [6]. In 2024, the crayfish industry in China maintained a strong development trend, with the farming area and production reaching 30.5 million mu (equals approximately 2.03 million hectares) and 3.45 million metric tons, respectively. Although the total annual revenue declined slightly, the overall consumer market remained stable, forming a three-pronged structure of catering, retail, and cultural tourism [42]. The industry provides livelihoods for millions of people, including farmers, processors, distributors, and retailers, particularly in regions where crayfish farming is a primary economic activity. The value chain associated with crayfish aquaculture encompasses various sectors, including feed production, equipment manufacturing, transportation, and marketing, further enhancing its economic significance [6]. Additionally, crayfish farming generates revenue through taxes, export earnings, and investment in infrastructure and technology, contributing to overall economic growth and development in China.

3.4.2 | Domestic Consumption Trends and Preferences

Domestic consumption of *P. clarkii* in China has experienced exponential growth in recent years, driven by changing consumer preferences, urbanization, and lifestyle trends (Figure 4) [6]. Crayfish consumption is deeply embedded in Chinese culinary culture, with a wide variety of dishes featuring crayfish as a central ingredient [5] (Figure 4). Popular cooking styles include spicy, garlic, and ginger-flavored crayfish, catering to diverse taste preferences across different regions. Urbanization and rising disposable incomes have further fuelled demand for crayfish products, with restaurants, street vendors, and online platforms offering a wide range of options to consumers [6]. Moreover, seasonal promotions and food festivals dedicated to crayfish contribute to spikes in consumption during peak harvesting periods, stimulating market demand and driving economic activity [78]. For example, during the Europe soccer championship in June–July 2024, the sales volume of *P. clarkii* increased over 20 times compared to other times in a supermarket in Nanjing [78].

3.4.3 | Export Markets and International Trade Dynamics

China's *P. clarkii* aquaculture industry has become increasingly integrated into global markets, with exports of *P. clarkii* products expanding to various countries and regions worldwide [6]. Key export markets for Chinese crayfish include Southeast Asia, North America, Europe, and the Middle East, where demand for freshwater crustaceans is growing due to their unique flavor and

culinary versatility [6]. In 2021, China's crayfish export volume reached 9693.9 tons, with an export value of nearly US\$120 million, a year-on-year increase of 27.6%. In 2024, both export volume and value remained comparable to those recorded in 2021 [42]. China's main export markets for crayfish are North America, Europe, and Japan, with the United States, Denmark, and the Netherlands ranking the top three [79]. International trade dynamics are influenced by factors such as trade policies, tariffs, sanitary and phytosanitary regulations, and consumer preferences [6]. China's competitive advantage in crayfish production, coupled with efficient logistics and distribution networks, positions it as a leading exporter in the global crayfish market [5, 6]. However, challenges such as market competition, quality control, and trade barriers may impact export performance and market access for Chinese crayfish exporters.

3.5 | Challenges and Constraints

The *P. clarkii* aquaculture industry in China faces a myriad of challenges and constraints, ranging from lack of improved breeds/varieties, environmental concerns, to socio-economic issues.

3.5.1 | Lack of Genetically Improved Breeds/Varieties of *P. clarkii* for Aquaculture in China

Although China has cultured the crayfish for food for over 40 years [5, 6], selective breeding programs targeting to

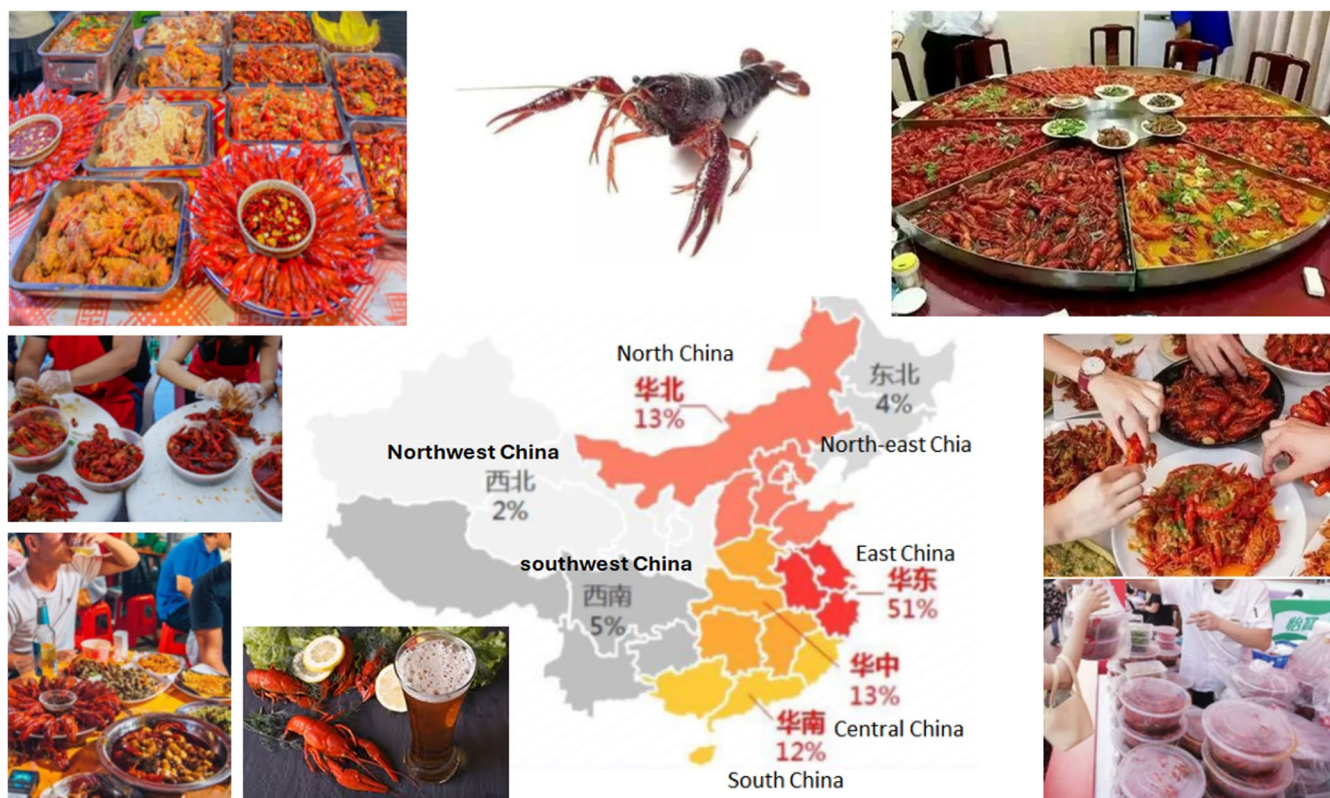


FIGURE 4 | Ways of domestic consumption of red swamp crayfish in China. In the middle, the map of China shows the major provinces and cities consuming red swamp crayfish. The numbers represent the proportion of consumption in different regions. Left and right pictures display different dishes and consumption ways (eating on sites or taken away) of the red swamp crayfish.

improve important production traits is still in their infancy [5, 6]. A few breeding programs for improving growth and stress tolerance are being carried out in some provinces. For example, “Xuyi No. 1” is a new improved variety of crayfish initially developed by the Jiangsu Provincial Freshwater Fisheries Research Institute using the conventional breeding technology and after six consecutive generations of breeding. The harvest weight of this breeding population has increased by 18.62%, and the yield per hectare has increased by 18.8% [80]. At present, this variety of crayfish has passed the evaluation by the National Aquatic Products Original Variety Approval Committee and approved a large-scale commercial production in China. The lack of enough genetically improved breeds/varieties of red swamp crayfish for aquaculture in China poses several challenges [6]. Firstly, it hinders the effective utilization of available germplasm resources, limiting the potential for increased productivity and economic returns. Secondly, self-propagation breeding has led to genetic degradation, resulting in smaller-sized crayfish with weaker disease resistance, impacting both quality and market demand. Additionally, the absence of genetically enhanced varieties restricts the ability to tailor breeding programs to address specific production needs, such as faster growth rates or improved feed conversion efficiency or improved omega-3 contents. This ultimately translates into higher production costs and reduced competitiveness in the global market. Therefore, accelerating genetic improvements of this species is critically important for sustainable and profitable crayfish aquaculture.

3.5.2 | Altering Local Freshwater Ecosystems due to *P. clarkii* Aquaculture

The *P. clarkii* is an invasive species known for its detrimental impact on local crayfish diversity in various regions around the world, including China [81, 82]. The *P. clarkii* outcompetes native species for resources such as food, shelter, and breeding sites [83]. Its rapid growth rate, high reproductive capacity, and aggressive behavior give it a competitive edge over native species [81, 83]. For example, in China, the *P. clarkii* has been observed displacing native species like the Chinese mitten crab (*Eriocheir sinensis*) from their habitats [84]. The *P. clarkii*'s ability to thrive in a wide range of environments, including freshwater bodies, wetlands, and rice fields, allows it to rapidly colonize and dominate ecosystems, pushing out other species in the process [85]. The *P. clarkii*, introduced to China, disrupts the balance and pushes out native species. *P. clarkii* is aggressive and has a varied diet, competing with native crayfish for food and shelter [3, 85]. This outcompetes the native species, leaving them with fewer resources to survive and reproduce. *P. clarkii* are omnivores and readily prey on the eggs and juveniles of native species. This disrupts the population cycles of native species, hindering their ability to maintain their numbers [86, 87]. For example, in Dianchi Lake, the introduction of the *P. clarkii* has led to the decline of the Dianchi crayfish (*Astacus tanggulaensis*). The *P. clarkii* outcompetes the Dianchi crayfish for food and habitat, and it is also a carrier of diseases that can harm native crayfish populations [86, 87]. In other countries, research reports have confirmed that due to the invasion and spread of *P. clarkii*, the native species of Scottish white crayfish in the southeastern

Spanish mountains has lost 90.0% of its available river habitat. In Portugal, due to the presence of *P. clarkii*, the success rate of the habitat reconstruction experiment for the native species of Scottish white crayfish was only 8.4%. Through the isolation and survival reconstruction experiment of the Scottish white crayfish habitat, it was found that when there is no *P. clarkii* in the habitat, the lost habitat of the Scottish white crayfish is likely to be restored [88]. Monosex production of *P. clarkii* is crucial to minimizing their impact on native crayfish populations and overall biodiversity. By producing only one sex, typically males, the risk of reproduction and establishment in the wild is reduced if they escape. This containment strategy helps control population growth, limiting the invasive species' ability to outcompete native crayfish and disrupt local ecosystems [89, 90]. Another way the *P. clarkii* reduces local crayfish diversity is through the transmission of diseases and parasites to native species [65]. The introduction of non-native pathogens can have devastating effects on vulnerable native populations that lack immunity to these diseases. For instance, in Costa Rica, *P. clarkii* populations have been found to carry pathogens such as the crayfish plague fungus (*Aphanomyces astaci*), which is lethal to many native crayfish species [91]. When infected *P. clarkii* meet native crayfish populations, they can spread the disease, leading to declines or even extinctions of native species. This could also happen in China.

3.5.3 | Ecological and Agricultural Impacts of Red Swamp Crayfish Burrowing

The red swamp crayfish caused significant ecological damage through its burrowing activities, especially in agricultural landscapes [19]. Its extensive burrowing weakens the structural integrity of terraced rice paddies, leading to water leakage, collapse of bunds, and reduced irrigation efficiency. These disruptions compromise rice production and increase maintenance costs for farmers [92]. Additionally, the crayfish can damage irrigation canals, levees, and embankments, undermining essential agricultural infrastructure. Beyond physical damage, its presence alters soil composition and hydrology, facilitating erosion and negatively impacting native aquatic organisms [92, 93]. In China, this issue may occur in provinces such as Hunan, Hubei, and Jiangsu, where rice-crayfish co-culture systems are common [94, 95]. However, based on our own observations over the past 20 years, the impact of crayfish burrowing on rice fields appears to be minimal. To date, there are no reports documenting serious effects on water conservancy, which may be due to a lack of relevant research. Additionally, crayfish typically burrow only under unfavorable environmental conditions, such as prolonged drought, low water availability, poor water quality (e.g., dissolved oxygen < 3 mg/L, polluted or eutrophic conditions), or extreme temperatures (above 35°C or below 10°C). Burrowing may also occur occasionally during molting or reproduction. During culture periods with good water quality, burrowing is not commonly observed in rice fields. To ensure the sustainable development of the crayfish aquaculture industry and to better understand its potential ecological and economic impacts, a systematic assessment of crayfish farming activities on domestic farmland water conservancy is urgently needed.

3.5.4 | Environmental Concerns and Habitat Degradation

One of the primary challenges confronting the *P. clarkii* aquaculture industry in China is the environmental impact associated with intensive farming practices [96]. High stocking densities and the extensive use of feed and fertilizers have led to water quality degradation, including increased nutrient levels and sedimentation in aquatic habitats [97]. Such environmental degradation not only threatens the health of crayfish populations but also compromises the overall ecosystem resilience. Furthermore, the expansion of crayfish farming has encroached upon natural habitats, leading to habitat loss and fragmentation, which further exacerbates environmental concerns [98, 99].

3.5.5 | Disease Outbreaks and Management Strategies

Disease outbreaks pose a significant threat to crayfish aquaculture operations in China, leading to substantial economic losses and production declines. Viral (e.g., white spot syndrome virus, WSSV), bacterial (e.g., *Aeromonas veronii* and *Citrobacter freundii*), and fungal (e.g., *Aphanomyces astaci*) pathogens have been identified as major culprits, causing mass mortalities and reduced productivity, causing mass mortalities and reduced productivity [41]. Despite efforts to implement biosecurity measures and disease management protocols, controlling outbreaks remains a significant challenge due to the complexity of aquatic ecosystems and the potential for pathogen transmission via waterborne routes. Developing effective disease prevention and control strategies is imperative for sustaining the growth of the crayfish aquaculture industry in China.

3.5.6 | Regulatory Issues and Policy Implications

The regulatory landscape governing *P. clarkii* aquaculture in China is complex, with a myriad of policies and regulations at the national, provincial, and local levels [5, 6]. Policymakers have promoted integrated rice-crayfish farming to boost rural incomes and alleviate poverty. This model, adopted in many regions, allows for dual harvesting of rice and crayfish, enhancing land use efficiency and farmer earnings [5, 6]. However, concerns have arisen about food security, as increased crayfish farming may reduce land available for winter crops. The invasive crayfish can outcompete native species for resources, disrupt habitats, and spread diseases, leading to a decline in native crayfish populations and overall biodiversity [100]. The *P. clarkii*, an alien species, has been farmed in China for over 40 years. Its escape from aquaculture sites into freshwater ecosystems poses a significant threat to local crayfish diversity [101]. Therefore, regulatory frameworks should adequately address emerging environmental and social concerns associated with crayfish farming, highlighting the need for policy reforms and greater stakeholder engagement to ensure sustainable development. Farmers benefit from higher incomes through integrated farming practices [5, 6]. For instance, in Qianjiang, farmers reported income increases from 60,000 yuan from four hectares of rice production a year to

250,000 yuan after adopting crayfish-rice co-cultivation [102]. Yet, they face challenges like market oversupply, which has led to price drops and profit concerns [103]. To mitigate this, investments in cold chain logistics and processing facilities have been made to extend sales periods and stabilize incomes. Consumers have driven domestic demand, making crayfish a popular delicacy across China. This surge in consumption has shifted the industry's focus from exports to satisfying local markets [5, 6]. E-commerce platforms have further facilitated access, with companies like JD.com and Alibaba purchasing large quantities to distribute nationwide.

Overall, while the crayfish industry's growth has brought economic benefits, it also presents challenges that require balanced approaches from all stakeholders to ensure sustainable development.

3.6 | Global Comparison of *P. clarkii* Aquaculture: China vs. the Rest of the World

China's *P. clarkii* industry towers over all others. Production rocketed to 2.96 million tons in 2022 and 3.45 million tons in 2024—about 95% of the world's farmed supply—thanks to huge rice-crayfish rotation ponds now spanning roughly 18 to 19 million ha and a tightly integrated value chain that can deliver live product overnight to coastal megacities [6, 104, 105]. Robust government extension, preferential credit, and e-commerce marketing have turned crayfish into a USD 60-plus billion domestic delicacy, while the recent ASC (Aquaculture Stewardship Council) certification of a Hubei paddy-crayfish farm signals China's push toward international sustainability standards [6, 104, 105]. Outside China, output is modest and fragmented [2]. Louisiana (USA) remains the epicenter; in normal seasons, 146,000 ha rice-crawfish ponds yield 80,000 to 90,000 tons worth about USD 500 million, although drought, saltwater intrusion, and a February 2024 cold snap slashed the latest crop [106]. Other US states, Egypt's Nile Valley, and small pockets in Spain, Italy, and Portugal depend largely on wild or semi-wild harvests that are tightly regulated because the species is classified as invasive, keeping annual national volumes in the low-thousand-ton range [2]. Profit margins therefore hinge on seasonal festivals and live-market premiums rather than year-round processing lines. Technological trajectories also diverge: China is already piloting genomic selection [107], automated graders, and chitin-astaxanthin biorefineries [6], whereas most non-Chinese producers focus on basic pond husbandry and niche live sales [2]. Consequently, China dictates global price, seed supply, and disease-control benchmarks, leaving the rest of the world as complementary, regionally important suppliers rather than true competitors.

4 | Research and Innovation for Genetic Improvement and Production

The *P. clarkii* aquaculture industry in China is characterized by extensive ongoing research and innovation efforts aimed at addressing key challenges and improving production efficiency while promoting sustainability and environmental stewardship [5].

4.1 | Recent Advancements in Breeding, Genetics and Genomics

Recent years have witnessed significant advancements in *P. clarkii* breeding and genetics, driven by a growing demand for improved traits such as growth rate, disease resistance, and tolerance to environmental stressors [5, 6]. Selective breeding programs have been instrumental in developing genetically improved strains with desirable traits, trying to enhance productivity and profitability for farmers [80]. Furthermore, advances in molecular genetics and genomic technologies have enabled researchers to gain insights into the genetic basis of important traits and accelerate the breeding process through marker-assisted selection (MAS) and genomic selection (GS) strategies [5]. These advancements hold great promise for further enhancing the genetic potential of crayfish populations and driving sustainable growth in the aquaculture industry.

4.1.1 | Developing DNA Markers

Microsatellites, being highly polymorphic, are used for population genetic studies, parentage analysis, and breeding programs. SNP markers, which are abundant and stable, facilitate genomic selection, genetic diversity assessment, and trait-linked marker development [108]. In China, DNA markers developed for the aquaculture of *P. clarkii* include microsatellites [32, 109] and single nucleotide polymorphisms (SNPs) [93, 110]. These molecular tools could enhance selective breeding efforts, aiming to improve growth rates, disease resistance, and overall productivity of *P. clarkii* in aquaculture settings.

4.1.2 | Establishing Molecular Parentage Technologies

The status of molecular parentage for *P. clarkii* aquaculture in China is advancing with the application of DNA markers such as microsatellites [37, 109] and single nucleotide polymorphisms (SNPs) [110]. These types of DNA markers enable accurate parentage analysis [32, 111], which is crucial for selective breeding programs. By identifying and tracking genetic relationships among individuals, breeders can enhance traits such as growth rate, disease resistance, and survival [112]. Molecular parentage analysis can improve the efficiency and effectiveness of breeding programs [113], leading to higher productivity and better management of genetic diversity in *P. clarkii* populations.

4.1.3 | Developing Genomic Resources

In China, the development of genomic resources [113] for the aquaculture of *P. clarkii* has significantly advanced in recent years [114]. Key genomic resources include whole-genome sequencing [13, 15], transcriptome analysis [115–117], and the identification of microsatellites [37, 109] and SNPs [110, 118] (Table 1). The genome of *P. clarkii* comprises 94 pairs of chromosomes. Its genome size is approximately 3.1 gigabases (Gb). The genome annotation has identified over 30,000 protein-coding genes [13, 15]. Whole-genome sequencing provides a comprehensive understanding of the genetic makeup of *P. clarkii*, facilitating the discovery of genes related to important traits such as growth [121], disease resistance [110], and environmental adaptation. This foundational resource

is crucial for various genomic studies and selective breeding programs. However, the draft genome of *P. clarkii* faces issues such as high heterozygosity, large genome size (~3.1 Gb), and abundant repetitive elements, complicating assembly and annotation. Solutions include using long-read sequencing (e.g., PacBio, Oxford Nanopore), Hi-C scaffolding for chromosome-level resolution, and advanced bioinformatics tools to resolve repeats and phase haplotypes more accurately.

Transcriptome analysis involves sequencing the RNA transcripts, offering insights into gene expression patterns under different conditions [129, 130]. This helps identify genes that are actively involved in physiological responses and developmental processes, contributing to a better understanding of the molecular mechanisms underlying important traits [123, 131–133]. Microsatellites and SNP markers are widely used in genetic diversity studies [4, 134], population structure analysis [93], and molecular breeding [111]. In the future, genomic databases and bioinformatics tools should be developed to store, manage, and analyze genetic data. These resources enable researchers and breeders to access and utilize genetic information effectively, facilitating improved breeding strategies.

4.1.4 | QTL Mapping and GWAS for Important Traits

In China, quantitative trait loci (QTL) mapping and genome-wide association studies (GWAS) have emerged as pivotal tools in the genetic improvement of aquaculture species, including *P. clarkii* [114, 135]. These approaches are instrumental in identifying the genetic basis of key traits such as growth rate, disease resistance, and environmental adaptation.

QTL mapping involves linking phenotypic traits to specific genomic regions [135]. This process has facilitated the identification of genomic loci associated with important traits, such as growth and sex determination in *P. clarkii* [121]. By using dense genetic maps constructed with microsatellite and SNP markers, researchers have pinpointed QTL that influence growth and sex determination [121, 136]. For example, in a study on QTL mapping for growth and sex determination, using 2b-RAD sequencing, a high-density genetic linkage map with 4878 SNP markers across 94 linkage groups was constructed. QTL mapping revealed 28 growth-related QTLs and identified candidate growth genes. A major sex determination locus on LG20 explained 59.3%–63.7% of variations, indicating a ZZ/ZW sex system. This study aids marker-assisted selection and genetic research in *P. clarkii* [121]. This information is crucial for MAS, allowing breeders to select individuals with desirable traits more efficiently. GWAS extends this effort by scanning the entire genome for associations between genetic markers and phenotypic traits [137, 138]. With the advent of high-throughput sequencing technologies, GWAS has become more feasible and powerful [138]. In *P. clarkii*, although the draft genome sequences of the *P. clarkii* has been published [13, 15], GWAS to identify SNPs linked to economically significant traits has not been carried out or published, probably due to the high cost of GWAS in crayfish species. GWAS is much more powerful in molecularly dissecting complex traits [135], thus enhancing our understanding of the genetic architecture of these traits and aiding in the development of genomic selection (GS) strategies. The integration of QTL mapping and

TABLE 1 | Representative genomic resources available for *Procambarus clarkii*, including DNA markers, linkage maps, genome sequences, and transcriptomes.

Genomic resource	Description	Details	References
DNA markers	Microsatellites	11 Microsatellites isolated from DNA libraries	[37]
		43,205 microsatellite sequences identified from transcriptome data.	[117]
		15 microsatellites used for genetic diversity analysis in three cultured populations.	[119]
	SNPs	4897 microsatellites developed based on genome survey sequencing	[120]
		4878 SNP markers used in a high-density genetic linkage map	[121]
		243,764 SNP sites identified from transcriptome sequencing of hepatopancreas, muscle, ovary, and testis	[117]
Linkage maps	High-density genetic linkage map	Contains 4878 SNP markers across 94 linkage groups, spanning 6157.737 cM, with 96.93% genome coverage	[121]
Genome Sequences	Genome Assembly	2.75 Gb genome size, contig N50 of 216.75 kb, 79.61% transposable elements, anchored to chromosomes using PacBio and Hi-C sequencing	[13]
		4.03 Gb genome size, N50 of 42.87 Mb, 91.42% anchored to 94 chromosomes, 70.64% repetitive sequences	[122]
		Estimated 8.50 Gb by flow cytometry, 1.86 Gb by Illumina sequencing, predicted 136,962 genes and 152,268 exons	[15]
Transcriptomes	In-depth transcriptome analysis	88,463 transcripts assembled (55,278 non-redundant) from hepatopancreas, muscle, ovary, and testis using HiSeq	[117]
	Gonadal development transcriptome	22,652 isotigs from testis and ovary libraries using 454 pyrosequencing, 1720 up- and 2138 down-regulated in ovary	[123]
	Eyestalk transcriptome	Transcriptome sequencing of eyestalk tissue to study neuroendocrine functions	[124]
	Intestine transcriptome (WSSV-infected)	125,394 contigs (normal) and 148,983 contigs (WSSV-challenged), 7000 DEGs identified	[125]
	Gills transcriptome (WSSV-infected)	172,591 contigs (normal) and 182,176 contigs (WSSV-challenged), 12,868 up- and 9194 down-regulated DEGs	[126]
	Ovary developmental stages transcriptome	Comparative analysis across developmental stages, identifying reproduction-related genes	[127]
	Growth rate transcriptome	122 growth-related DEGs	[128]

Abbreviations: DEGs: differentially expressed genes; Gb: one gigabase (Gb) equals 1 billion base pairs; Hi-C sequencing: a method to study the 3D structure of genomes by mapping chromatin interactions genome-wide, revealing how DNA sequences interact in space; HiSeq: name of a next-generation sequencing platform; SNP: single nucleotide polymorphism; WSSV: white spot syndrome virus.

GWAS could significantly advance selective breeding programs for *P. clarkii* in China. These methodologies enable precise genetic improvement, leading to enhanced growth rates, improved disease resistance, and better overall productivity. Consequently, the use of these genomic tools is expected to continue driving advancements in the aquaculture of *P. clarkii*.

4.1.5 | Developing Molecular Sexing Technologies

In China, sex-linked DNA markers have been developed for molecular sexing of *P. clarkii* [121, 139]. Two papers published by two groups revealed different results [121, 139]. In one paper, it was reported that the sex determining system in *P. clarkii* is XY-system [139, 140]. The paper claimed that a DNA marker located on the XX chromosome (i.e., LG38) was able to differentiate sex with a high precision (99.49%) in 196 crayfish collected from five different geographic regions [140]. Another paper reported that the sex-determining system in *P. clarkii* is a ZW system [121]. A major sex determination locus was identified in LG20, explaining 59.3% to 63.7% of phenotypic variations. In addition, SNPs associated with sex were identified [121]. The XY sex-determining system was confirmed by a recent paper [140]. According to our own recent research on sex determination in the crayfish (unpublished data), the sex determination system in *P. clarkii* is XY. Therefore, we believe it is highly likely that *P. clarkii* has an XY sex-determining system. Therefore, these sexing markers published [121, 139, 140] allow for the identification of sex-specific genetic differences, enabling early and accurate determination of the sex of individual crayfish. The application of sex-linked DNA markers streamlines the breeding process and enhances the overall productivity of *P. clarkii* aquaculture in China. To make the molecular sexing more precise, it is essential to identify the sex-determining genes using QTL mapping, GWAS, and gene functional analysis as carried out in the fighting fish [141] and tilapia [142].

4.1.6 | Developing Genome Editing Technologies

Genome editing with CRISPR/Cas systems involves using a guide RNA to direct the Cas9 enzyme to a specific location in the DNA [143]. Once there, Cas9 creates a double-strand break, allowing for precise modifications by adding, deleting, or altering genetic material. This technology enables targeted and efficient genetic changes in various organisms [144]. Genome editing in crayfish is emerging but not as advanced as in other species [114]. In China, efforts are focused on developing CRISPR/Cas9 techniques to improve traits such as growth rate, disease resistance, and environmental adaptability [114]. However, many studies are primarily in the experimental phase, with no successful gene knockouts reported yet. Globally, similar trends are seen, with researchers in the US and Europe exploring CRISPR applications for ecological studies and aquaculture improvements [144]. Despite these advances, practical applications are limited, and further research on *P. clarkii* is needed to overcome challenges like efficient delivery systems and off-target effects. Genome editing in crayfish using CRISPR/Cas systems presents several challenges. First, obtaining one-cell fertilized eggs is difficult due to the crayfish's reproductive biology [7, 21]. This stage is critical for effective genome editing but is complicated by the asynchronous nature of egg maturation and fertilization. Second, microinjection of the

Cas9-gRNA complex into these eggs is technically challenging. The small size and hard chorion of crayfish eggs make it difficult to introduce the editing mixture without damaging the embryo. Solutions include optimizing protocols for synchronizing egg maturation and improving in vitro fertilization techniques to reliably obtain one-cell stage embryos. Advanced microinjection techniques and equipment, such as piezoelectric injectors [145], can enhance precision and reduce embryo damage. Additionally, alternative delivery methods, like electroporation or viral vectors [146], can be explored to bypass the difficulties of direct microinjection. These advancements could potentially improve the efficiency and success rates of genome editing in crayfish. The application of genome editing in the red swamp crayfish raises several concerns, including potential ecological risks if edited individuals escape into the wild and disrupt native populations. Ethical issues surrounding genetic manipulation and animal welfare also warrant attention. Additionally, regulatory frameworks for genome-edited aquatic species remain unclear in many regions, posing challenges for approval and public acceptance. Long-term impacts on biodiversity and ecosystems must be carefully evaluated before widespread application.

4.2 | Disease Control and Management

Disease control and management of *P. clarkii* aquaculture in China have been a focus of attention due to the species' commercial significance [6, 29]. Scientists are studying the biology and epidemiology of various diseases [9, 147–149] that affect crayfish, aiming to develop effective detection [150], prevention, and treatment strategies [151]. Genetic approaches are being used to identify disease-resistant strains [152], while research on environmental factors and management practices that impact disease outbreaks is also underway [41]. Researchers have been conducting studies to assess genetic diversity and population structure to facilitate selective breeding and improve disease resistance [4, 81, 134, 153]. Additionally, monitoring of potential pathogens and implementing preventive measures, such as maintaining water quality and controlling the introduction of new stocks, is crucial for disease management [154]. Although challenges exist, such as the emergence of new diseases and the need for continued research, the industry has made strides in enhancing disease control and management practices to ensure sustainable aquaculture of *P. clarkii* in China. Collaboration between researchers, farmers, and industry stakeholders is fostering the exchange of knowledge and best practices, ultimately contributing to the sustainable development of *P. clarkii* aquaculture in China.

4.3 | Developing Feeds and Optimizing Feeding Schemes

Research on developing feeds and optimizing feeding schemes for *P. clarkii* aquaculture in China has gained significant momentum in recent years. Scientists are exploring various ingredients and formulations to create balanced diets that promote optimal growth, health, and disease resistance in crayfish [63, 155, 156]. Research focuses on understanding the nutritional requirements of crayfish at different life stages and incorporating locally available and sustainable feed resources [157]. Additionally, studies are being conducted to optimize feeding frequencies, quantities, and timing

to maximize growth performance and reduce waste. Through the research on nutritional requirements, feed formulation, and feeding strategies—such as stage-specific diets and automated feeding systems—growth rates, survival, and overall productivity have improved, enhancing the sustainability and profitability of crayfish farming [5]. This research is crucial for the sustainable and profitable development of *P. clarkii* aquaculture in China.

4.4 | Technologies for Improving Production Efficiency

Technological innovations play a crucial role in improving production efficiency and reducing environmental impact in crayfish aquaculture operations. Automation and sensor technologies have been increasingly utilized to monitor water quality parameters, optimize feeding regimes, and manage farm operations more efficiently [158]. Furthermore, the adoption of RAS and integrated multitrophic aquaculture (IMTA) practices has enabled farmers to minimize water usage, reduce waste discharge, and maximize resource utilization, thereby enhancing sustainability and profitability [51]. Additionally, the development of novel feed formulations incorporating alternative ingredients and supplements [40, 61, 62, 157] has the potential to improve feed conversion efficiency and reduce reliance on traditional feed sources, contributing to cost savings and environmental sustainability.

4.5 | Sustainable Practices and Environmental Stewardship Initiatives

In response to growing environmental concerns, the *P. clarkii* aquaculture industry in China has increasingly focused on implementing sustainable practices and environmental stewardship initiatives [5, 6]. Efforts to minimize environmental impact include the adoption of best management practices for water and land use, the implementation of effluent treatment systems, and the restoration of degraded aquatic habitats. Moreover, industry stakeholders have collaborated with research institutions and government agencies to develop certification schemes and eco-labeling programs that recognize and reward environmentally responsible aquaculture practices [56, 97]. These initiatives not only help mitigate environmental risks associated with crayfish farming but also enhance market competitiveness and consumer confidence in sustainably sourced crayfish products.

5 | Future Directions and Recommendations

As the *P. clarkii* aquaculture industry in China continues to evolve, it is essential to identify future directions and provide recommendations to guide its sustainable and profitable growth and development (Figure 5).

5.1 | Opportunities for Further Growth and Development

Despite facing numerous challenges, the *P. clarkii* aquaculture industry in China remains poised for further growth and development [56, 96]. The increasing demand for crayfish both

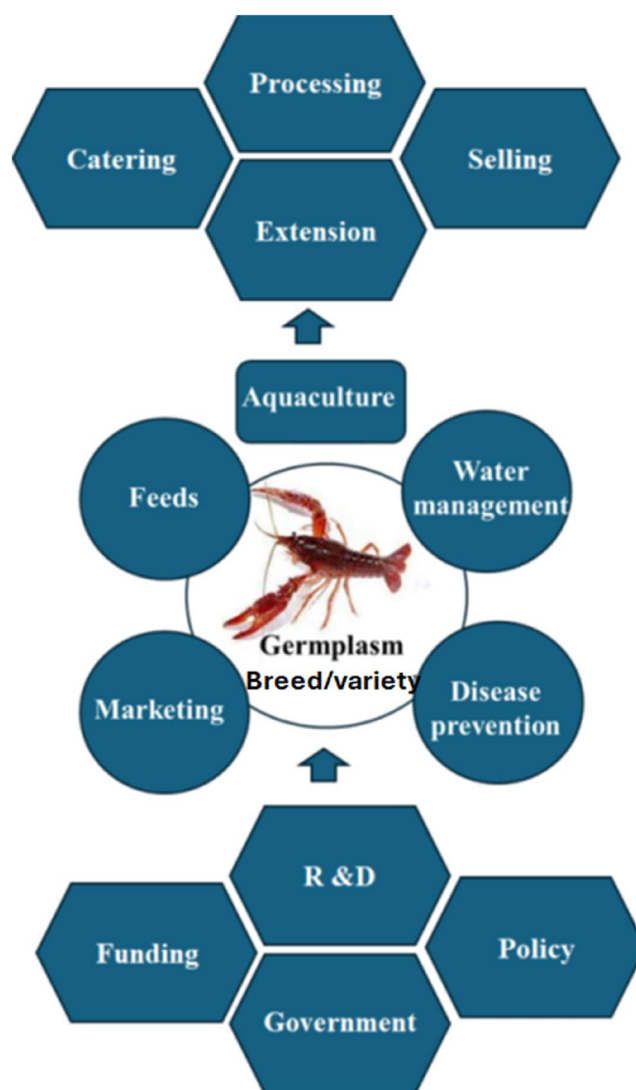


FIGURE 5 | A strategic roadmap for developing a sustainable and profitable aquaculture industry for the red swamp crayfish (*Procambarus clarkii*), highlighting key milestones, innovations, pathways for long-term growth and environmental stewardship and building related secondary and tertiary industries that support, process, and commercialize the primary production.

domestically and internationally presents significant opportunities for expanding production and market penetration [5, 6]. Additionally, advancements in technology, such as selective breeding [159], MAS [135], GS [137] and genome editing [144] offer avenues for improving production efficiency, reducing environmental impact, and enhancing product quality. Furthermore, the integration of crayfish farming with other agricultural activities, such as rice-crayfish cultivation [14, 97] or crayfish-tilapia co-culture [160] through indoor farming [50], RAS, and IMTA systems [161] can unlock synergies and maximize resource utilization, contributing to the sustainable development of rural economies.

5.2 | Priorities for Research and Innovation

The research and innovation priorities for the aquaculture of red swamp in China can be summarized in the following aspects.

5.2.1 | Genetic Improvement for Important Traits

The *P. clarkii* is an alien species and was introduced to China in the 1920s. Although many studies on genetic diversity of crayfish populations have been conducted in different regions and using different DNA markers, including mitochondrial DNA, microsatellites, and SNPs [4, 81, 134], there is no overall picture of genetic diversity in populations in China. Therefore, it is essential to use a standard DNA marker set as those recommended by FAO to assess global genetic diversity in livestock [162, 163], to access the genetic diversity in *P. clarkii* to set a solid foundation for selective breeding using molecular technologies, including parentage, QTL mapping, GWAS, MAS, and GS. Genetic improvement for economic traits, including growth, disease resistance, feed conversion ratio, and stress tolerance, is a critical step for sustainable and profitable aquaculture [164]. With the improved quality of life people care more about food quality and nutritional values. Therefore, improving omega-3 fatty acids in crayfish meat may be an important trait for genetic improvement using various breeding approaches, including MAS, GS, and genome editing.

5.2.2 | Improving Aquaculture Technology and Production Systems

It is essential to improve aquaculture technology and production systems to increase the productivity and profitability of crayfish aquaculture [5]. Further exploring symbiotic aquaculture models combining *P. clarkii* with rice, Chinese mitten crabs, lotus roots, and other crops to achieve resource recycling may reduce environmental pollution and the carbon footprint of crayfish aquaculture [6, 42]. Feed is the major cost for crayfish aquaculture [165]; therefore, developing specialized feeds with balanced nutrition and low costs to improve the growth rate and quality of *P. clarkii* is an urgent need for genetically improved breeds/varieties.

5.2.3 | Optimization of Aquaculture Environment

It is essential to protect aquatic systems by optimizing the aquaculture environment for *P. clarkii*. By improving containment measures and water quality management [166], the risk of crayfish escaping into natural habitats is minimized. In addition, monosex production technologies [89, 90] should be developed for this species to prevent multiplication of this crayfish in local freshwater systems to protect endemic crayfish and fish species. These measures could help prevent the disruption of local ecosystems, protect native species, and maintain biodiversity, ensuring sustainable aquaculture practices and environmental conservation.

5.2.4 | Disease Prevention and Control, and Immune Enhancement

To enhance disease prevention and control, as well as immune enhancement in *P. clarkii*, several strategies are essential. First, establishing a monitoring system for diseases is crucial to promptly detect and control outbreaks, ensuring quick responses to potential threats [150]. Additionally, developing safe and effective immune enhancers [167] will strengthen the crayfish's immunity, thereby reducing the incidence of diseases.

Furthermore, employing biological control techniques, such as using natural enemies, microorganisms, and other biological methods [90], can effectively prevent and control diseases while minimizing the reliance on chemical drugs. These approaches collectively contribute to healthier crayfish populations and more sustainable aquaculture practices.

5.2.5 | Waste Management and Resource Utilization

Effective waste management and resource utilization in *P. clarkii* aquaculture are essential. Researching harmless treatment technologies can reduce environmental pollution from waste [5, 6]. To improve sustainability and profitability in crayfish aquaculture, the wastes such as shells can be fully utilized in various ways. The shells are rich in chitin, which can be processed into chitosan, a valuable biopolymer with applications in medicine, agriculture, and water treatment [168]. Chitosan can be used for wound dressings, biodegradable films, and as a natural pesticide. Additionally, crayfish shells can be used to produce calcium supplements for animal feed, improving livestock health. The shells can also be converted into biofertilizers, enriching soil with essential nutrients [169]. Furthermore, they can serve as biofilters in aquaculture systems, helping to maintain water quality by adsorbing heavy metals and other pollutants [170]. These approaches not only reduce waste but also create new revenue streams, enhancing the overall sustainability and economic viability of crayfish farming.

5.2.6 | Market Expansion and Brand Building

Market expansion and brand building for *P. clarkii* involve several key strategies. Conduct in-depth research on domestic and international market demand trends to guide aquaculture production [6]. Strengthen brand development and marketing efforts to enhance market visibility and competitiveness. Additionally, research processing technologies to develop deep-processed products, extending the industrial chain and increasing product value added.

5.2.7 | Informationalization and Intelligent Aquaculture

To advance informationalization and intelligent aquaculture, employ Internet of Things (IoT) technology to monitor environmental parameters for intelligent management [171]. Collect data from the aquaculture process and use big data analysis to inform decision-making. Additionally, develop smart equipment, such as automatic feeders and water quality monitors [172], to enhance the efficiency of *P. clarkii* aquaculture.

6 | Conclusion

The review of the crayfish aquaculture industry in China has shed light on various aspects, including its historical development, status, challenges, and opportunities. The industry has experienced remarkable growth over the past few decades, fueled by increasing demand for crayfish both domestically and

internationally. However, this growth has been accompanied by environmental, social, and economic challenges, such as habitat degradation, disease outbreaks, and socio-economic disparities in rural communities. Despite these challenges, the industry has demonstrated resilience and innovation, with ongoing efforts focused on research, technology adoption, and sustainability initiatives. Looking ahead, the future of *P. clarkii* aquaculture in China hinges on the adoption of sustainable practices, technological innovation, and policy reforms. Addressing environmental concerns, enhancing disease management strategies, and promoting genetic improvement will be critical for ensuring the long-term viability and resilience of the industry. Moreover, leveraging advancements in improving production efficiency through technological innovation and fostering collaboration between industry stakeholders, research institutions, and policymakers will be essential for driving continued growth and competitiveness in the global market.

Author Contributions

G.H.Y., Z.X., and B.L.: conceptualization; data curation; writing – original draft; writing – review and editing. **G.H.Y.:** formal analysis; funding acquisition; investigation; methodology; project administration; resources; software; supervision; validation; visualization.

Acknowledgments

This work was supported by the internal fund of the Temasek Life Sciences Laboratory, Singapore. We are very grateful to Ms. Joey Wong for editing the English of this paper.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

All data are from published papers cited in this paper.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Table S1:** Transport methods of red swamp crayfish juveniles and newly hatched larvae for production and their advantages.