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REVIEW

REVIEWS IN Aquaculture

Innovation and development of the aquaculture nutrition research and feed industry in China

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Abstract

Aquaculture in China has undergone significant evolution in recent decades, transitioning from traditional practices to a vital food production industry. Alongside the rapid growth of aquaculture in China, aquafeed production continues to expand swiftly. This review attempts to establish an overview of the history and achievements in aquaculture nutrition research and feed industry in China. The development of scientific concept and methodology, especially the advanced molecular biology technology guarantees the shift from traditional nutrition to molecular nutrition, and subsequently to precision nutrition in aquaculture nutrition research. This evolution has facilitated the formulation of effective strategies to enhance the growth, health and product quality of aquatic animals. The advancements of aquaculture nutrition research and feed industry have also been propelled by innovative research concepts rooted in principles such as the health and safety of aquatic animals, the quality of aquatic products, resource conservation and environmental friendliness, and the advancements in key processing technologies within the aquafeed industry. The future perspectives of the aquaculture nutrition research and feed industry in China are also proposed. The present work aims to provide a reference for promoting the development of aquaculture nutrition research and feed industry in China.

KEYWORDS
aquafeed industry, development status, feed ingredients, innovation, research concept, research methods

1 | INTRODUCTION

Over the last few decades, aquaculture in China has evolved from a traditional practice to a crucial food production sector, accounting for more than half of global food fish consumption.[1] According to the statistics of the Food and Agriculture Organization, people is now consuming more aquatic food than ever before, with about 20.2 kg of aquatic products per person in 2020, which is more than double the amount consumed 50 years ago.[2] In 2020, global fisheries and aquaculture production reached a record high of 178 million tons.[2] Although total production of global fisheries and aquaculture has increased rapidly over the past two decades, the production from wild capture has stabilized,[2] indicating the booming development of farmed fisheries. The global aquaculture production has seen a remarkable increase from 2.6 million tons in 1970 to 87.5 million tons in 2020.[2] Therefore, the development of efficient and sustainable aquaculture can provide a food supply for humans and contribute to the global 'blue transition' in aquaculture.

China plays a significant role in global aquaculture, contributing approximately 60% of the world's total aquaculture production.[2]

Aquaculture production in China has risen from 2.33 million tons in 1978 to 53.94 million tons in 2021, a 20-fold production increase over the past few decades (Data from China Fisheries Statistical Yearbook 1979–2022). This rapid expansion of aquaculture has outpaced the availability of traditional feed sources, such as natural baits and low-value ingredients, necessitating the development of the aquafeed industry to support sustainable growth of aquaculture. Therefore, the goal of this paper is to provide a broad overview of the current knowledge and prospects for the aquaculture nutrition research and feed industry in China to inform the future development of the aquaculture nutrition research and feed industry. Notably, because of the great diversity of aquaculture species in China, it would be futile to attempt to review the current knowledge in the aquaculture nutrition research and feed industry of all these species. What is endeavoured here is to illustrate with suitable examples, where appropriate, and to illustrate the breakthrough in research methodology, research concept and key technologies, and prospects of aquaculture nutrition research and feed industry in China.

2 | HISTORY OF THE AQUAFEED INDUSTRY IN CHINA

Aquaculture has been practiced for millennia. Early on, people would keep fish collected from rivers, lakes and the seas in captivity and use them as food reserves. Oracle bone inscriptions discovered from the Shang Dynasty in Yin Ruins of Henan Province (1395–1123 BCE) indicated that fish farming was being practiced during this period. Clay depictions of carp ponds, as well as writings by Fan Li in China around 500 BCE (Chinese Aquaculture Society[3]), further document aquaculture activities. Until the 1950s, aquaculture in China relied on capturing wild fingerlings for stocking ponds, and depending on natural food resources within the ponds to provide nutrients for the fish. However, overfishing from increased population growth has greatly reduced the production of wild fish. For small-scale farmer (the single most populous group in the world), fewer resources are available to them, and thus many terrestrial and aquatic macrophytes are used in aquaculture, and this mode of culture is also widely used in other Asian and developing countries.[4] Moreover, there was a lack of research on aquaculture nutrition in China, so agricultural byproducts were used as feeds based on fish nutrition data published abroad.[5] However, due to the limited understanding of nutrient requirements, the feed conversion ratio was high. Since the 1980s, universities such as Sun Yat-sen University, Ocean University of China, and Shanghai Ocean University started to offer fish nutrition courses. Pioneers of aquaculture nutrition in China, such as Professors Ding Lin, Aijie Li, Daozun Wang, and so forth, played a prominent role in recruiting and supervising postgraduate students in this field. At the same time, many research institutes and feed enterprises have joined efforts to conduct systematic research on the nutritional requirements of major aquaculture species in China and the bioavailability of feed ingredients. These collective efforts led to significant improvements in the quality of aquafeeds developed in China. As a result, aquafeed enterprises emerged, and the aquafeed industry in China experienced substantial development. Overall, the history of aquaculture nutrition in China has seen a progression from a reliance on natural productivity to the systematic study of nutritional requirements and the development of improved aquafeeds. This has played a crucial role in supporting the growth and development of the aquaculture in China.

After 20th century, the demand for aquafeeds increased rapidly. However, Chinese aquaculture is highly diverse in terms of culture species, feeding habits, ecological distribution, and culture mode. Due to the late inception of aquaculture nutrition research, limited research funding, and a shortage of nutrition research experts, it is difficult to quantify the nutritional requirements of such a diverse range of species, even within an extended timeframe. To address these challenges, Chinese governmental departments and researchers in the field of aquatic nutrition collaborated to propose the selection of representative species, standardize research methods, and conduct systematic studies. Accordingly, a comprehensive database of nutrient requirements for representative aquatic species (Figure 1) in China was developed. The insights garnered from researching these representative species were subsequently extrapolated to other farmed species with similar taxonomic status, geographic distribution, feeding habits, and farming modes. Subsequently, a database of nutritional parameters for major aquatic animals in China was gradually emerged,

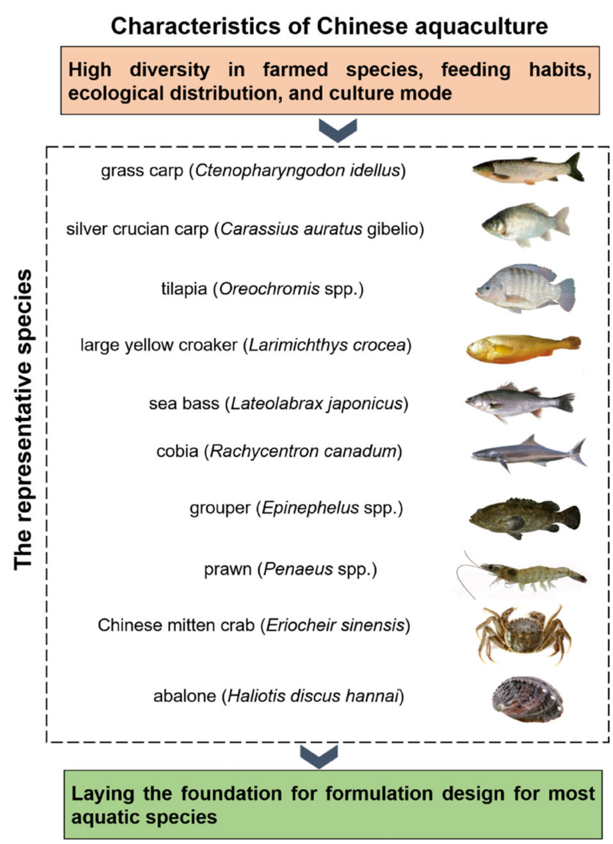


FIGURE 1 The representative aquatic species in China after 20th century.

which plays a crucial role in promoting the development of feed industry.

In the 21th century, aquaculture nutrition research has been facilitated by increased research funding, a growing number of aquaculture nutrition professionals, and international cooperation. Especially in the past decade, there has been a significant increase in funding from programs such as National Key Research and Development Program of China, the National Natural Science Foundation of China, and feed enterprise funding, which provided strong support for discipline construction and the development of the aquafeed industry. Scientists and feed industry also hope to improve the health of farmed animals by offering high-quality feed products, ensuring food safety, and safeguarding the farming environment, all with the overarching goal of fostering sustainable development of aquaculture. Overall, these advancements in aquaculture nutrition research have led to the improvement of aquafeed quality, the promotion of healthy and sustainable aquaculture practices, and the further development of the aquaculture in China.

3 | PRODUCTION OF AQUACULTURE AND AQUAFEED IN CHINA

Over the past four decades, aquaculture production in China has increased rapidly along with the production of aquafeeds. The aquafeed industry in China began in the 1980s and has since witnessed significant expansion. In 1991, the production of aquafeed in China was only 7.5×10^5 tons but it reached 2.3×10^7 tons in 2021, an increase of about 30 times in 30 years (Figure 2). Nonetheless, a notable disparity persists between the total aquafeed production and the total aquaculture yield in China. While there are farming models that do not rely heavily on formulated feeds, such as rice-fish co-culture and filter-feeding fish farming, there is immense potential for further development of aquafeeds in China. The spatial profiles of aquaculture and aquafeed production in China varies significantly by region (Figure 3). For example, the volume of aquaculture and aquafeed in the east and south regions was much higher than in the north and west areas. Guangdong, Shandong, Fujian, Hubei, and Jiangsu are the top five provinces for aquaculture production with annual outputs of 7.57, 6.42, 6.32, 4.81 and 4.33 million tons, respectively. Collectively, these provinces represent over half of the total production nationwide.[6] The pattern of the change in the regional distribution of aquafeed production is similar to that of aquaculture. Guangdong, Jiangsu, Hubei, Fujian, and Hunan are the top five provinces of aquafeed production with annual outputs of 7.49, 3.61, 2.63, 1.67 and 1.34 million tons, respectively. These provinces contribute over 70% of the total aquafeed production nationwide (data source: China Feed Industry Association, http://www.chinafeed.org.cn/). The high aquafeed production in these regions can be attributed to the relatively high aquaculture production levels, creating a greater demand for aquafeed. Additionally, these regions have a longer history in the aquafeed industry and are home to several large feed enterprises, such as Guangdong HAID Group Co., Ltd., Guangdong Yuehai Feeds Group Co., Ltd., and Guangdong Evergreen Feed Industry Co., Ltd.

4 | CURRENT ACHIEVEMENTS OF THE AQUATIC ANIMAL NUTRITION AND FEED INDUSTRY IN CHINA

4.1 | Scientific breakthroughs in research methodology

With the development of aquaculture as a major industry, methods of research in aquaculture nutrition have undergone huge changes, evolving from the classical gradient nutrient approach to physiological and biochemical analyses and molecular biology methods. This shift has allowed researchers to gain a deeper understanding of the specific mechanisms of nutritional metabolism in aquatic animals. In general, traditional nutritional research methods are extensive, but few studies related to the specific mechanism of nutritional metabolism have been conducted. In the traditional conception of aquaculture nutrition

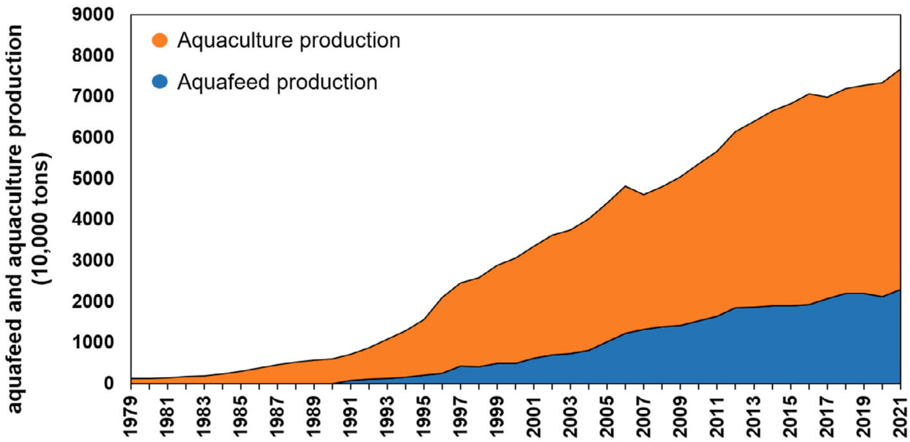
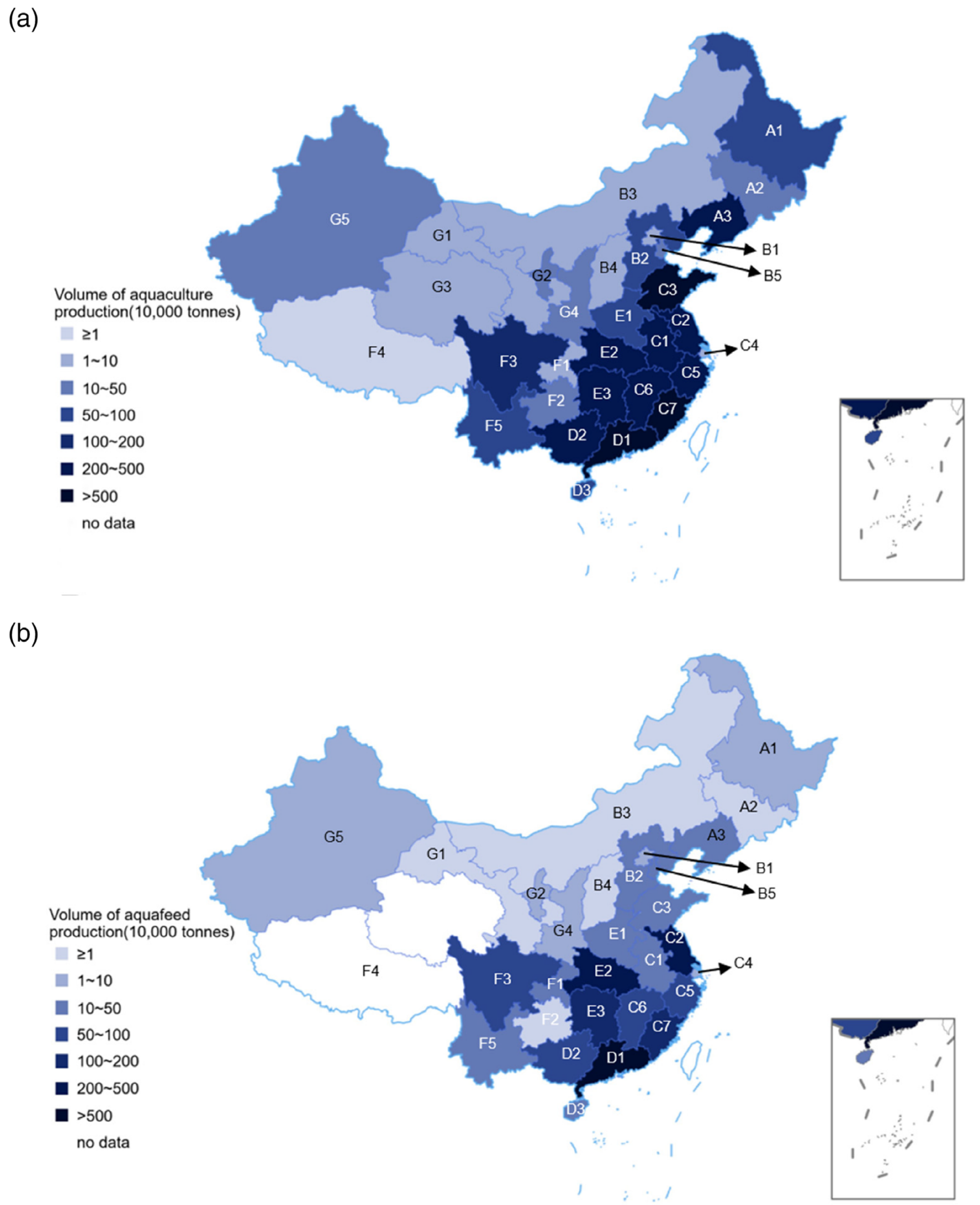


FIGURE 2 The aquafeed and aquaculture production in China 1978–2021. *Data Source*: Fishery Bureau of Ministry of Agriculture PRC (1979–2022) and China Feed Industry Association (http://www.chinafeed.org.cn/).



Region		1	2	3	4	5	6	7
Northeast	A	Heilongjiang	Jilin	Liaoning				
North	B	Beijing	Hebei	Inner Mongolia	Shanxi	Tianjin		
East	C	Anhui	Jiangsu	Shandong	Shanghai	Zhejiang	Jiangxi	Fujian
South	D	Guangdong	Guangxi	Hainan				
Central	E	Hennan	Hubei	Hunan				
Southwest	F	Chongqing	Guizhou	Sichuan	Tibet	Yunnan		
Northwest	G	Gansu	Ningxia	Qinghai	Shaanxi	Xinjiang		

FIGURE 3 Regional distribution of aquaculture production (a) and aquafeed production (b) (except for Hong Kong, Taiwan and Macau) in 2021. (a) The aquaculture production volume for each province; (b) the aquafeed production volume for each province. Data source: Fishery Bureau of Ministry of Agriculture PRC (2022)[6] and China Feed Industry Association (http://www.chinafeed.org.cn/).

research, an increase in growth is regarded as a direct indicator of good nutritional status in aquatic animals. In the past, nutritionists usually determined the nutrient requirements of aquatic animals through feeding trials, using mathematical models to analyse indicators such as growth and nutrient composition in the whole-body and tissues of aquatic animals.[7–9] However, with the increasing demands for the health and quality of fish products in intensive aquaculture, there is a need to explore nutrient metabolism and related signalling pathways in order to achieve precise nutrient regulation and meet the demand for high-quality aquatic products. For example, researchers have identified multiple molecular targets involved in nutrient deposition and health regulation in fish, such as mechanistic target of rapamycin (mTOR),[10] adenosine 5′-monophosphate (AMP)-activated protein kinase (AMPK),[11] farnesoid X receptor (FXR),[12] and NF-E2-related factor 2 (Nrf2),[13] nuclear factor Kappa B (NFκB)[14] and transcription factor EB (TFEB).[15] Over the past decades, aquaculture nutrition research has moved from traditional nutrition to molecular nutrition and then to precision nutrition.

4.2 | Innovation in the concept of aquaculture nutrition research

With the improvement of the living standards of humans, the quality and safety of aquatic products have attracted more attention. Simultaneously, aquaculture nutrition research has become more focused on the concept of resource conservation and environmentally friendly aspects.

4.2.1 | Animal health and safety of aquatic products

The use of antibiotics has raised concerns about antibiotic resistance and the presence of drug residues in animal tissues, posing risks to human health.[16,17] In aquaculture, approximately half of the production loss is caused by disease.[18] Disease outbreaks in fish, which result in significant economic losses, are often linked to environmental pollution and nutritional imbalances that weaken the immunity of aquatic animals.[19,20] By exploring clear mechanisms, nutritional and non-nutritional regulation strategies have been developed to enhance the immunity of farmed aquatic animals, improve their health, increase survival rates, reduce drug usage, and ensure the quality and safety of aquatic products. For example, toll-like receptors 22 (TLR22) have been found to recognize dsRNA in the cell membrane, activating inflammatory responses in macrophages of large yellow croaker (*Larimichthys crocea*) through the nuclear factor kappa B and type I interferon pathways. Furthermore, docosahexaenoic acid (DHA) has been shown to attenuate TLR22-triggered inflammation by reducing the contents of membrane sphingomyelins and saturated fatty acid-containing-phosphatidylcholines, which are necessary for lipid raft organization.[21] DHA could alleviate palmitic acid-induced inflammation in macrophages via the TLR22-MAPK-PPARγ/Nrf2 pathway in *L. crocea*.[22] Vitamin D could attenuate *Aeromonas hydrophila* induced inflammation via vitamin D receptor b/macrophage stimulating 1 by modulating NFκB and signal transducer and activator of transcription 3 signalling pathway in grass carp (*Ctenopharyngodon idella*).[23] Nutrition and immunology have become hot topics in aquaculture nutrition.[24] In recent years, Chinese researchers have focused on the synergistic effects of nutrition and immunity, the relationship between malnutrition and disease, the relationship between nutrients (energy, protein, amino acids, fatty acids, vitamins and minerals) and the cellular differentiation and cellular metabolites of the immune system, as well as the nutritional requirements for maintaining optimal immune function in aquatic animals under various stressful conditions.[25] Immuno-enhancing agents used in aquafeeds in China include vitamins, trace elements, oligosaccharides, nucleotides, and Chinese herbs to enhance the immunity of aquatic animals.[26–30] However, there is still a need for more in-depth research on nutrition and immunity in aquaculture in China, as well as a better understanding of the immunomodulatory mechanisms of functional additives.

4.2.2 | Quality of aquatic products

The quality of fish flesh is a complex set of characteristics that can be affected by intrinsic and extrinsic factors.[31] Numerous studies have demonstrated that flesh quality is closely related to nutrition, and that feeding improper nutrients or ingredients can lead to a significant reduction in the flesh quality and flavour of farmed fish.[32–34] Therefore, it is important to study the mechanisms by which nutrition controls the quality of aquatic products, and on this basis develop additives that can improve the quality of aquatic products.

Many recent studies have shown that there are differences in the ability of marine and freshwater fish to synthesize highly unsaturated fatty acids. The omega-3 fatty acids such as eicosapentaenoic acid (EPA) and DHA are known for their beneficial effects on human health and disease prevention.[35] The elongase 5 of rainbow trout has a higher degree of chromatin opening and promoter activity than that of large yellow croaker, which may explain the freshwater fish's higher capacity for synthesizing EPA and DHA.[36] Moreover, previous studies have also demonstrated that the Nrf2 and mTOR pathways may be involved in the regulation of the nutritional quality and flavour of muscle in fish.[32,37] These mechanistic insights serve as valuable references for the developing functional additives and the utilizing nutrients to enhance the quality of aquatic products.

Generally, the quality of aquatic animals is markedly affected by different nutrients or ingredients in feeds. For instance, replacing fishmeal with alternative protein sources, such as animal protein sources, plant or fermented plant protein sources, insect protein sources, or single-cell protein sources, can have varying degrees of negative impact on the flesh quality of different farmed fish.[38–45] Previous studies have demonstrated that high-fat diets (HFDs) can reduce the flesh quality of Nile tilapia (*Oreochromis niloticus*).[46,47] In contrast, Zhang et al.[46] reported that increasing lipid catabolism by supplementing with L-carnitine can rectify the increased pH and hardness in fillets caused by HFD in *O. niloticus*. Moreover, substituting an appropriate proportion of vegetable oil for fish oil in feed can improve the flesh quality properties (liquid holding capacity, TBARS value, and overall flavour score) of *L. crocea*.[48] Suitable amounts of lipid sources or essential fatty acids, especially n-3 high unsaturated fatty acids, in the diets of aquatic animals can improve the flesh quality and flavour.[49,50] Excessive amounts of carbohydrates, another important macronutrient, in the diet can also significantly reduce the fibre diameter, pH, liquid holding capacity, and hardness of muscle tissue of olive flounder *Paralichthys olivaceus*.[51] Additionally, micronutrients such as vitamins A, C, and E, folic acid, riboflavin, thiamin, minerals, as well as some functional additives including L-carnitine, tea polyphenols, oligosaccharides, and Chinese herbs, have been found to play important roles in regulating flesh quality and/or flavour in aquatic animals.[46,52–63]

4.2.3 | Resource conservation

Aquaculture has emerged as the largest consumer of global fishmeal, accounting for 68% of annual production.[64] Fishmeal is widely used as an animal protein source in the aquafeed due to its appropriate palatability and high nutritional value.[65] However, the scarcity of fishmeal as a premium protein source has led to rising prices, necessitating the search for alternative protein sources. In recent years, studies worldwide have focused on finding potential substitutes for fishmeal.[65–68] We searched the web of science database (https://www.webofscience.com/) using the keywords 'fishmeal substitution' and 'aquaculture'. We found 820 papers published over the last decade, 21.95% of which were published by Chinese research institutions (Figure 4a). It is clear that China has made a significant contribution in finding potential alternatives to fishmeal. Investigations on substituting plant protein ingredients for fish meal have attracted the most attention (Figure 4b). Various plant-based ingredients, such as soybean meal and cottonseed meal, have been used as fishmeal alternatives in aquafeed due to low market price and sustainable production.[69,70] However, the use of plant-based ingredients also has many limitations, such as the existence of anti-nutritional factors, strong reliance on arable land, fertilizer, and water, and competition for food with humans. Consequently, China has focused on developing cost-effective and sustainable non-traditional sources.[71–73]

Microbial fermentation and enzymatic digestion have been used to improve poor palatability, low digestibility, imbalanced amino acid composition, and high anti-nutritional content in non-traditional protein sources. Fermentation with specific microorganisms can help preserve nutrients, reduce feed costs, and minimize environmental pollution associated with plant protein sources.[74] Animal processing by-products can also be hydrolysed using various proteolytic enzymes to produce protein hydrolysate rich in essential nutrients and bioactive peptides.[75] Tables 1 and 2 summarize the fermented plant protein sources and enzymatic protein ingredients used for aquafeed in China. Nevertheless, there are challenges to be addressed, such as implementing technological advancements in large-scale feed production and investigating the physiological and health effects of fermented and enzymatic protein feeds on aquatic animals.

Apart from plant-based alternatives, aquaculture by-products, insect meals, macroalgae, and single-cell proteins have been investigated as fishmeal substitutes in aquafeed.[64,72,76–79] In China, there has been a notable emphasis on single-cell proteins, particularly one-carbon molecular gas protein (C1GP). C1GP is derived from bacterial fermentation using environmentally sustainable substrates sourced from waste streams or industrial C1 molecular gases, such as methane, methanol, CO, and CO_2.[80,81] C1GP is a promising protein source due to its high-level protein, ideal amino acid profile, and low carbon emissions. The most commonly used types of C1GP in China currently include methanotroph bacteria meal (*Methylococcus capsulatus*) and *Clostridium autoethanogenum* meal. Wang et al.[72] reviewed microorganisms, protein production technology, nutrition, products utilizing C1 gases, and their aquafeed applications. Dietary methanotroph (*M. capsulatus*, Bath) bacteria meal (FeedKind®) improved growth, digestibility, and antioxidant capacity of juvenile Jian carp (*Cyprinus carpio* var. Jian).[82] *M. capsulatus* meal replaced up to 30% fish meal without significantly negative effects on growth performance and health of juvenile turbot.[83] Dietary *C. autoethanogenum* protein regulated energy homeostasis in juvenile farmed tilapia (GIFT: *O. niloticus*) via adenosine 5′-monophosphate (AMP)-activated protein kinase pathway.[84] *C. autoethanogenum* protein replaced up to 42.80% of dietary fish meal without adverse effects on growth and flesh quality of largemouth bass (*Micropterus salmoides*).[39] Synthetic biotech-produced single-cell protein sources offer advantages, not competing

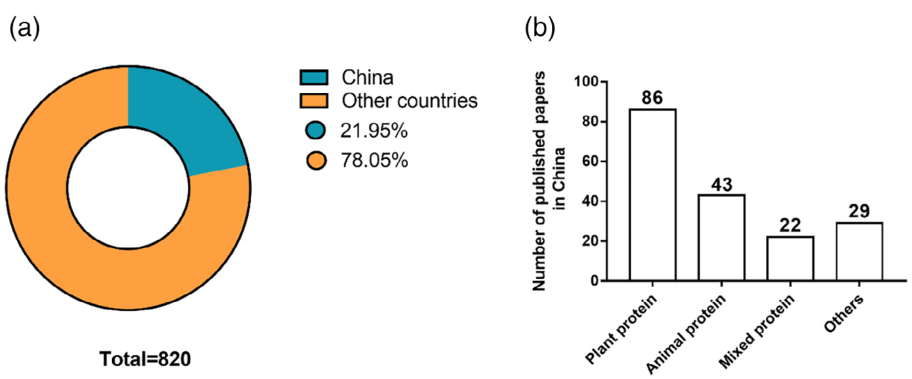


FIGURE 4 The number of papers on fish meal substitution published by scientific institutions in China and other countries outside China. (a) The total number of published papers; (b) The number of published papers on fish meal substitution with different protein sources. Mixed protein including plant protein sources and animal protein sources; Others including single-cell proteins such as yeast, Chlorella, and one-carbon molecular gas protein.

TABLE 1 Fermented plant protein sources for aquafeed in China.

Aquatic animals	Plant protein	Microorganism	Appropriate supplemented level	References
Turbot (*Scophthalmus maximus* L.)	Soybean meal	*Lactobacillus plantarum* P8	34.62%	Wang et al.[110]
Pacific white shrimp (*Litopenaeus vannamei*)	Soybean meal	*Bacillus subtilis* E20	44.43%	Shiu et al.[111]
Pacific white shrimp (*L. vannamei*)	Cottonseed meal	*B. subtilis* BJ-1	20.60%	Sun et al.[112]
Macrobrachium nipponense	Soybean meal	Mixture of microorganism (*Pediococcus acidilactic*, *Enterococcus aecalis*, *Saccharomyces cerevisiae*, *Candida utilis*, *B. subtilis*, *Bacillus licheniformis*, *Rhodopseudomonas palustri*).	20.00%	Ding et al.[113]
Black sea bream (*Acanthopagrus schlegelii*)	Soybean meal	*C. utilis*	14.40%	Zhou et al.[114]
Pacific white shrimp (*L. vannamei*)	Soybean meal	*Lactobacillus* spp.	<30.90%	Lin and Mui[115]
Black sea bream (*A. schlegelii*)	Cottonseed meal	*B. subtilis* BJ-1	16.00%	Sun et al.[116]
Crucian carp (*Carassius auratus gibelio*)	Mushroom bran hydrolysate	*Ganodermalucidum* and *S. cerevisiae*	6.40%–8.00%	Zhang et al.[117]
Red tilapia (*Oreochromis mossambicus* × *Oreochromis niloticus*)	*Enteromopha prolifera*	*Lactobacillus acidophilus* and *S. cerevisiae*	3.70%–4.10%	Yang et al.[118]
Pompano (*Trachinotus ovatus*)	Soybean meal	—	10.00%	Lin et al.[119]
Gibel carp (*Carassius auratus gibelio* var. CAS V)	Mixing of rapeseed meal, sprayed corn husk, rice bran, palm meal, and soybean meal	*Lactobacillus* spp. and *Bacillus* spp.	5.00%	Cao et al.[120]
Largemouth bass (*Micropterus salmoides*)	Soybean meal	*B. subtilis* and *Lactobacillus*	15.68%	He et al.[121]
Hybrid groupers (*Epinephelus fuscoguttatus*♀ × *Epinephelus lanceolatus*♂)	Rice protein	*Aspergillus oryzae*	5.98%	He et al.[122]
Nibea diacanthus	Soybean meal	—	19.65%–22.73%	Li et al.[123]
Large yellow croaker (*Larimichthys crocea*)	Soybean meal	—	25.46%	Wang et al.[124]
Snakehead (*Channa argus* × *Channa maculata*)	Soybean meal	—	7.20%	Duan et al.[125]
Largemouth bass (*M. salmoides*)	Soybean meal	*B. subtilis* and *Lactobacillus* spp.	9.00%	Jiang et al.[126]
Turbot (*Scophthalmus maximus* L.)	Soybean meal	*Saccharomycopsis fibuligera* isolate Y27, *Bacillus tequilensis* KCTC 13622, *B. subtilis* strain D7XPN1 and *Bacillus aryabhattai* B8W22	—	Dan et al.[127]

for human food, needing minimal resources, and contributing to the concept of sustainable development by repurposing waste.

There is growing evidence that the use of insect protein ingredients in aquafeeds is a sustainable alternative in worldwide including China. Insects such as black soldier fly (*Hermetia illucens*), yellow mealworm (*Tenebrio molitor*), and common housefly (*Musca domestica*) have high productivity and fast life cycles, yielding high quality and readily assimilated proteins and highly unsaturated fatty acids, as well as vitamins and functional compounds.[85] Numerous studies have shown that the appropriate level of insect protein in feed has the functions of promoting growth, antioxidant capacity, immunity, liver and intestinal health, regulating nutrient metabolism and intestinal flora of aquatic animals. Table 3 summarize the black soldier fly meal, yellow mealworm meal, and common housefly meal used for aquafeed in China. Although the application of insect proteins in aquatic feeds has shown promising results, however, there are still many constraints on

TABLE 2 Enzymatic animal processing by-products for aquafeed in China.

Aquatic animals	Source of hydrolysate	Enzyme used for preparing hydrolysate	Appropriate supplemented level	References
Turbot (*Scophthalmus maximus*)	By-products of pollock *Theragra chalcogramma*	—	<10.80%	Wei et al.[128] and Wei et al.[129]
Japanese flounder (*Paralichthys olivaceas*)	Frames of pollock *Theragra chalcogramma*	Alcalase and flavourzyme	3.70%	Zheng et al.[130]
Turbot (*Scophthalmus maximus*)	Frames of pollock *Theragra chalcogramma*	Alcalase and flavourzyme	—	Zheng et al.[131]
Japanese sea bass (*Lateolabrax japonicus*)	Gut and head of pollock *Theragra chaloogramma*	Protease	8.10%	Liang et al.[132]
Large yellow croaker (*Pseudosciaena crocea*)	Tissues of pollock *Theragra chalcogramma*	Flavourzyme and Alcalase	10.00%	Tang et al.[133]
Turbot (*S. maximus*)	Feather meal and blood meal of poultry	—	8.00%	Hao et al.[134]
Turbot (*S. maximus*)	Chicken by-product	—	2.00%	Zhuang et al.[135]

the development of insect proteins in aquatic feeds, such as the reasons for the differences in the effects of insect proteins on different aquatic animals, and how to obtain greater economic benefits based on the protection of fish health, which are worthy of more in-depth research.

4.2.4 | Environmentally friendly

Protecting the aquatic environment and ensuring the sustainability of aquaculture is another important goal for aquaculture in China. In the past, wild fish or low-quality artificial formulated feeds were used to feed aquatic animals, leading to excessive nitrogen and phosphorus excretion and pollution of the aquatic environment. In intensive, high-density aquaculture, the amount of residual bait and excreta exceeds the decomposition capacity of microorganisms, resulting in increased nitrogen and phosphorus concentrations in water, deterioration of water quality, and eutrophication. This ultimately causes dysregulation of the material and energy cycle of the aquaculture system.[86] Recently, there has been a shift towards optimizing feed formulations to improve nutrient utilization and reduce excessive nitrogen and phosphorus excretion. A previous study reported that exogenous enzymes, including phytase and non-starch polysaccharide enzymes, in diets reduced the nitrogen and phosphorus excretion of Japanese seabass (*Lateolabrax japonicus*).[87] Diets with phytase supplementation improved the utilization of minerals and reduce the phosphorus excretion of rainbow trout (*Oncorhynchus mykiss* Walbaum).[88] Meanwhile, diets with 1500 U/kg phytase could improve growth and decrease the nitrogen and phosphorus excretion of Channel catfish (*Ictalurus punctatus*).[89]

Multiple influences of antibiotics in various aquatic animals, including decreased[17,90,91] and increased growth performance,[92,93] body malformation,[94] microbiota dysfunction,[93,95] induced oxidative stress[96,97] and decreased immunity.[98,99] More importantly, one study reported a direct human health risk linked to the consumption of fish treated with antibiotics in children.[99] In recent years, aquatic nutritionists have conducted many studies related to mitigating the harmful effects of antibiotics on aquatic animals through nutritional strategies, such as using cellulose and increased carbohydrate level in diets.[17,100] However, in general, there are relatively few studies exploring the relationship between nutrition and the environment in aquaculture in China.

4.3 | Progression in key processing technologies of the aquafeed industry

Based on advances in research methods and innovations in research concepts, breakthroughs have been made in key processing technologies such as feed pre-digestion techniques and extruded feed technology in the aquafeed industry. The feed pre-digestion techniques include physical pre-digestion, chemical pre-digestion, and biological pre-digestion technologies, which aim to break down large molecules into small molecules for improved digestion and absorption.[101] Physical pre-digestion technology is accomplished through water, heat, mechanical, or other physical processes, such as cutting short of ingredients, de-mixing, steam granulation, extruding, steaming and microwaving. Chemical pre-digestion uses chemical reagents such as acid and alkali to treat ingredients in the diet, including alkaline treatment, ammonia treatment and oxidation treatment. Biological pre-digestion is the treatment of feed ingredients by enzymatic or microbial fermentation techniques to improve feed digestibility. The use of feed pre-digestion technology can eliminate most of the toxic and harmful substances and anti-nutritional factors in feeds, reduce the stress of antigens in feeds on the intestines of aquatic animals, and improve the feed utilization of aquatic animals.[101] The use of feed pre-digestion technologies can also improve the utilization rate of non-conventional feed resources while making full use of cottonseed meal, rapeseed meal, and other plant-based protein sources to alleviate the shortage of feed ingredients in China.

TABLE 3 The application of black soldier fly meal, yellow mealworm meal, and common housefly meal in aquafeed in China.

Type of products	Aquatic animals	Experimental design	Appropriate supplemented level	Growth effect	Change of nutritional composition	Other effects	References
Black soldier fly pulp	Mirror carp (*Cyprinus carpio* var. specularis)	Fish meal substitution	13.1%	—	↓Whole-body lipid content	↑Antioxidant capacity	Xu et al.[136]
Black soldier fly pulp	*Micropterus salmoides*	Diets supplementation	2%	↑	↓Liver lipid content	Damage in the liver and intestine	Peng et al.[137]
Black soldier fly larvae meal	Grass carp (*Ctenopharyngodon idella*)	Fish meal substitution	3%	60% substitution level: ↓	—	—	Huang et al.[138]
Black soldier fly larvae meal	Jian carp (*Cyprinus carpio* var. Jian)	Fish meal substitution	14%	—	—	—	Zhou et al.[139]
Black soldier fly larvae meal	Yellow catfish (*Pelteobagrus fulvidraco*)	Fish meal substitution	10%	↑ first, then ↓	↓ first, then ↑ whole-body lipid content	↑immunity	Xiao et al.[140]
Defatted black soldier fly larvae meal	Pacific white shrimp (*Litopenaeus vannamei*)	Fish meal substitution	23.40%	—	>60% substitution level: ↓whole-body protein content	>60% substitution level: atrophy of the hepatopancreatic vesicles	Wang et al.[141]
Defatted black soldier fly larvae meal	Japanese seabass (*Lateolabrax japonicus*)	Fish meal substitution	14.40%	—	—	—	Wang et al.[142]
Black soldier fly larvae meal	Large yellow croaker (*Larimichthys crocea*)	Fish meal substitution	14.0%	↑ First, then ↓	↑Whole-body lipid content ↓whole-body protein content	↑Antioxidant capacity	Han et al.[143]
Defatted black soldier fly larvae meal	Jian carp (*Cyprinus carpio* var. Jian)	Fish meal substitution	10.60%	—	↓Whole-body lipid content	↑Antioxidant capacity	Li et al.[144]
Zymolytic black soldier fly pulp	Largemouth bass (*Micropterus salmoides*)	Diets supplementation	1.00%	↑	—	↑Antioxidant capacity ↑disease resistance	Xu et al.[145]
Yellow mealworm meal	Nile tilapia (*Oreochromis niloticus*)	Fish meal substitution	8.40%	—	↓Whole-body protein content	>45% substitution level: ↑hardness and gumminess of muscle ↓springiness of muscle	Zhang et al.[146]
Yellow mealworm meal	Large yellow croaker (*Larimichthys crocea*)	Fish meal substitution	17.05%	60% substitution level: ↓	100% substitution level: ↓muscle lipid content ↑muscle protein content	>60% substitution level: ↓activity of intestinal digestive enzymes >75% substitution level: ↓texture and flavour	Yuan et al.[147]
Yellow mealworm meal	Yellow catfish (*Pelteobagrus fulvidraco*)	Fish meal substitution	18.00%	—	—	↑immunity and bacterial resistance	Su et al.[148]

(Continues)

TABLE 3 (Continued)

Type of products	Aquatic animals	Experimental design	Appropriate supplemented level	Growth effect	Change of nutritional composition	Other effects	References
Yellow mealworm meal	Pearl gentian grouper (*Epinephelus lanceolatus* ♂ × *Epinephelus fuscoguttatus* ♀)	Fish meal substitution	4.92%	>12% substitution level: ↑		>25% substitution level: ↓disease resistance	Song et al.[149]
Yellow mealworm meal	*Macrobrachium rosenbergii*	Diets supplementation	5.01%	↑	↓Lipid content in the muscle and carcass ↑protein content in the muscle and carcass	↑Immunity	Feng et al.[150]
Yellow mealworm meal	Mirror carp (*Cyprinus carpio* var. specularis)	Soybean meal substitution	11.47%–11.94%	↑	>45% substitution level: ↑muscle protein content >60% substitution level: ↑whole-body protein content	↑Muscle fibre diameter	Li et al.[73]
Yellow mealworm meal	Largemouth bass (*Micropterus salmoides*)	Fish meal substitution	4.00%	33% substitution level: ↓	—	>11% substitution level: ↑immunity and antioxidant capacity	Gu et al.[78]
Defatted yellow mealworm meal	Large yellow croaker (*Larimichthys crocea*)	Fish meal substitution	6.70%	45% substitution level: ↓	45% substitution level: ↑whole-body moisture	↑intestinal health	Zhang et al.[151]
Maggot meal	Yellow catfish (*Pelteobagrus fulvidraco*)	Fish meal substitution	13.73%	>40% substitution level: ↓	—	100% substitution level: ↓antioxidant capacity	Yang et al.[152]
Maggot meal	Black carp (*Mylopharyngodon piceus*)	Diets supplementation	4.20%–5.00%	—	—	↑antioxidant capacity ↑immunity	Liu et al.[153]
Housefly maggot meal	Pacific white shrimp (*Litopenaeus vannamei*)	Fish meal substitution	22.08%	>80% substitution level: ↓	↓Whole-body lipid content	>60% substitution level: ↓immunity	Cao et al.[154]
Maggot meal	Nile tilapia (*O. niloticus*)	Fish meal substitution	10.00%	—	>60% substitution level: ↓whole-body lipid content	>60% substitution level: ↑antioxidant capacity	Shi et al.[155]

Compared with livestock feed, aquafeed has higher requirements in terms of crushing size, steam conditioning, and pellet appearance. Since the 1990s, extruded feed technology has been widely used in the global aquafeed industry, bringing profound changes to the aquafeed development in China. Investigations related to extruded feeds are also being conducted on many aquatic animals in China.[102–106] The feed extrusion process is carried out under high temperatures and pressure, leading to physical and chemical changes such as starch pasting, protein denaturation, and inactivation of enzymes, toxic components, and microbes. These changes enhance feed digestibility,[106] reduce anti-nutritional factors, such as trypsin inhibition factor in soybeans, gossypol in cottonseed, and glucosinolate in rapeseed, and so forth, and microorganisms in feed, as well as improve feed palatability and the stability in water.[107,108] However, the high temperatures and long heating duration associated with the extrusion process can reduce the digestibility of protein and amino acids and damage heat-sensitive substances (e.g., vitamins A, E, and C; polyunsaturated fatty acid).[104] The Maillard reaction caused by lysine reacting with reducing carbohydrates or carbonyl compounds can also result in the loss of lysine and reduced protein biological potency.[109] Therefore, it is necessary to evaluate the effects of different extrusion conditions on the utilization of nutrients, determine the most suitable extrusion conditions, and improve the post-spraying technology. Breakthroughs in these key processing technologies are essential for achieving efficient and sustainable aquaculture practices. Regarding feed processing equipment, initially, China heavily depended on imported aquafeed machinery. Moreover, there were limited sets of feed equipment suitable for aquaculture in China. In fact, specific livestock and poultry feed machinery were imported and then adapted for aquafeed production. Over time, feed machinery manufacturing industry in China has achieved substantial advancement, ensuring the production capacity of aquafeed through ongoing introduction and innovation.

5 | CONCLUSIONS AND FUTURE PERSPECTIVES

The evolution of aquaculture in China, transitioning from a traditional practice to a thriving food production sector, has been accompanied by significant advancements in aquaculture nutrition research and the development of the aquafeed industry. This work highlights the journey of aquaculture nutrition research and feed industry in China, emphasizing key achievements and future directions. In China, aquaculture nutrition research has transitioned from relying on natural productivity to a comprehensive understanding of nutritional requirements and mechanisms of nutrient metabolism in aquatic animals. Notably, this transformation has been facilitated by methodological breakthroughs and conceptual innovations within aquaculture nutrition research. These advancements have enriched our understanding of nutrient metabolism in aquatic animals and have facilitated the formulation of effective strategies to enhance growth, health, and product quality. The concept of aquaculture nutrition research in China has shifted towards resource conservation, environmental friendliness, and the production of high-quality aquatic products. Meanwhile, advanced processing technologies dramatically improved feed quality, digestibility, and nutrient utilization in aquatic animals, bolstering the sustainable aquaculture.

The aquaculture nutrition research and feed industry in China is suggested to develop in the direction of environmental friendliness, safety, intelligence, and cost-effectiveness. Additional research and applied technological approaches may need to be strengthened in following areas: (1) searching for non-food protein sources such as C1GP, insect protein source, and agriculture by-products that do not compete for human food resources, and reducing dependence on imports of fishmeal and soybean meal; (2) exploring the relationship between nutrition and the environment, and laying the foundation for the development of formulated feeds that reduce nitrogen and phosphorus emissions and represent an alternative to antibiotics; (3) developing digital and intelligent nutrition and feed application systems, such as intelligent feed analysing and processing equipment, and large-scale baiting systems, consistent with the development of aquaculture models such as recirculating water aquaculture and deep-sea aquaculture; (4) strengthening the multidisciplinary cross-collaboration of animal nutrition and genetic breeding in aquaculture.

AUTHOR CONTRIBUTIONS

Qinghui Ai: Resources; writing – review and editing; supervision; project administration; funding acquisition. **Xianyong Bu:** Writing – original draft; writing – review and editing. **Yueru Li:** Writing – review and editing. **Wencong Lai:** Writing – review and editing. **Chuanwei Yao:** Writing – review and editing. **Yongtao Liu:** Writing – review and editing. **Zhen Wang:** Writing – review and editing. **Zengqi Zhao:** Writing – review and editing. **Shangzhe Han:** Writing – review and editing. **Jianlong Du:** Writing – review and editing. **Xin Yao:** Writing – review and editing. **Kangsen Mai:** Resources; supervision.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

This work was based on previously published research; no primary data were used.

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