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The Future of Aquatic Protein: Implications for Protein Sources in Aquaculture Diets

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Approximately 70% of the aquatic-based production of animals is fed aquaculture, whereby animals are provided with high-protein aquafeeds. Currently, aquafeeds are reliant on fish meal and fish oil sourced from wild-captured forage fish. However, increasing use of forage fish is unsustainable and, because an additional 37.4 million tons of aquafeeds will be required by 2025, alternative protein sources are needed. Beyond plant-based ingredients, fishery and aquaculture byproducts and insect meals have the greatest potential to supply the protein required by aquafeeds over the next 10–20 years. Food waste also has potential through the biotransformation and/or bioconversion of raw waste materials, whereas microbial and macroalgal biomass have limitations regarding their scalability and protein content, respectively. In this review, we describe the considerable scope for improved efficiency in fed aquaculture and discuss the development and optimization of alternative protein sources for aquafeeds to ensure a socially and environmentally sustainable future for the aquaculture industry.

Introduction

The growth of the human population leading into the middle of the 21st century poses significant challenges to the supply of high-quality, nutrient-rich food whereby a population of 9.7 billion by 2050[1] will require an increase in the supply of food by 25%–70%.[2] This is all in the face of a deteriorating natural resource base and competing interests for agriculturally based input commodities.[3] Concurrent with population growth is the "rise of the middle class," whereby increased affluence (mainly in China and southeast Asia) comes with a shift to diets that incorporate an increasing proportion of protein from animal sources.[4–6] Although livestock food sectors are intensifying production in an attempt to meet demand, this comes with significant challenges including overgrazing, water shortages, and loss of natural biodiversity.[3,7,8] It is now recognized that the farming of aquatic species (i.e., aquaculture) will provide an increasingly significant component of the global animal-derived protein budget. In fact, aquaculture has been the fastest growing food production sector by annual growth rate over the last three decades, with annualized growth rates of 10% in the 1990s and 5.8% yearly between 2000 and 2016.[9] On an edible animal-source food basis, sector growth is second only to poultry.[10]

Aquaculture production can be classified as "unfed" or "fed." Unfed aquaculture relies on supplying animals (e.g., filter-feeders such as silver carp, grass carp, and bivalves) with food from the production ecosystem itself.[11] Fed aquaculture is the largest and fastest growing component of the sector (excluding seaweeds) and usually involves supplying animals with formulated aquafeeds or whole or processed fish. The diets of fed species have historically relied on high concentrations of fish meal (protein source) and fish oil (lipid source, typically rich in long-chain polyunsaturated fatty acids of the omega-3 series) derived from the capture of small pelagic fish, known as forage fish (Box 1). Unfortunately, the rapid rise of aquaculture has placed a significant amount of pressure on forage fish stocks,[12] whereby a peak in the wild fisheries production volume was reached in 1995 followed by a consistent decline.[13] At the same time, global fish consumption is increasing at a rate of 1.5% per year on a per capita basis and wild fisheries currently are static.[9] This raises concerns regarding the disruption of aquatic food webs and the sustainability of supply of this global commodity, whereby about 10% of fish biomass caught from wild-capture fisheries is used to feed high-value, and often carnivorous, species.[9] High-value product is commonly exported to affluent countries, reflected in the value of seafood trade between global regions (Figure 1). However, the estimated domestic consumption of aquaculture production volume in 2011 was 85%–89% among the top ten aquaculture-producing countries (representing 87% of global aquaculture production, 51% of the total population, and 52% of the undernourished population),[14] highlighting the importance of aquaculture (unfed and fed) for the provision of protein for human consumption (Figure 1). As such, the future expansion of the aquaculture industry is critical for sustained human nutrition, and a balance between the expanding production of resource-intensive carnivorous species and the continued production of high-yielding, low-value species (e.g., herbivores or detritivores) that support local communities is required[15] (Figures 1 and 2).

Although the production of fish meal and fish oil from forage fish has been steadily decreasing over the last 20 years and the proportion of these ingredients within aquafeeds is demonstrating a downward trend, they are still important feed components for many carnivorous fishes and crustaceans.[26] The total

Box 1. Components of Aquafeeds beyond Dietary Protein

Fish are valuable sources of nutrients and micronutrients, and play an important role in human nutrition and the global food supply.[9,16,17] In addition to being a rich source of high-quality protein and essential amino acids, fish are a dietary source of health-promoting omega-3 or n-3 long-chain polyunsaturated fatty acids (LC-PUFA), eicosapentaenoic acid (EPA) and docosahexaenoic acid (DHA), essential minerals (calcium, phosphorus, zinc, iron, selenium, and iodine), and vitamins (A, B, and D).[9] Even with increased prevalence of alternative ingredients in aquafeeds, fish products from aquaculture must continue to maintain the levels of these fatty acids and micronutrients for healthy and nutritious human diets.[9,18]

Modern aquafeeds are a sophisticated, engineered mix of ingredients (raw materials) that provide the nutritional requirements that facilitate the intensive and efficient production of aquaculture species. These raw ingredients include commodity meals, oils, vitamins, pigments, minerals, and concentrates, which, when combined, satisfy an organism's demand for macronutrients and micronutrients. In addition, these ingredients ensure rapid rates of growth, support animal health, and, importantly, result in a product with sensory and quality properties that meet consumer demands.

Traditionally, forage fish have been the foundation ingredient of aquafeeds, as they contain high-quality protein, micronutrients, and lipids, and are an important source of LC-PUFA. In addition to finding alternative sources of protein to alleviate the pressure on forage fish, we recognize that alternative sources of micronutrients and lipids will be essential.[18,19] Fish-oil use in aquaculture is projected to increase by ~14% due to the growing demand in the marine finfish and crustacean aquaculture sectors as they expand.[9,20,21] As such, global fish-oil supply is one of the limiting factors for the aquaculture feed industry.[18,19,22] Alternative lipid sources to fish oil include vegetable oils, animal fats, single-cell oils, algae oils, transgenic oils, and fish byproduct oil.[18,22] However, discussions of alternative lipid and micronutrient sources are beyond the scope of this review.

annual production of fish meal was ~4.5 million tons, and the total annual production of fish oil s ~0.9 million tons in 2016, of which 69% and 75%, respectively, are used in aquafeeds.[20] An additional 23% and 5% of this fish meal is used in pig and chicken feeds.[20] Notably, the total production of aquafeeds for all aquaculture species is predicted to increase by 75% from 49.7 million tons in 2015 to 87.1 million tons in 2025[11] (Figure 2). The volume of wild-caught forage fish required for this increase is unattainable based on current feed formulations, while uncertainty of future access to this resource is a key issue. The availability of sustainably fished small pelagics for fish meal and oil has not increased in 24 years,[13] and their inclusion levels in aquafeeds must be decreased at a greater rate for aquaculture to provide an increasingly large proportion of healthy seafood to an expanding global population. A variety of plant protein ingredients (e.g., soybean meal, corn gluten meal, rapeseed meal) and animal byproducts (e.g., meat and bone meal, poultry meal) are being used as alternative protein sources to fish meal in aquafeeds. While these terrestrial, plant-based proteins (e.g., soy concentrate) will continue to be important components of aquafeeds, they have significant limitations, often containing anti-nutritional elements, and the industry itself has limited potential to expand production without putting additional stress on land, water, and phosphorous resources.[27] As such, to meet the demand of the additional 37.4 million tons of aquafeeds required by 2025, finding alternative, cost-effective sources of protein is critical. In this review we consider emerging, alternative feed ingredients to replace the protein provided by forage fish and highlight the opportunities and challenges to their implementation. We also suggest areas for improved efficiencies in aquaculture through breeding and disease resistance and suggest future directions to support the rapid and sustainable growth of the aquaculture industry.

Fishery and Aquaculture Byproducts

Fishery and aquaculture byproducts are the raw materials that remain after the industrial-scale processing of fish for human consumption. After processing, between 50% and 70% of the byproducts are considered "inedible" and typically consist of trimmings (i.e., viscera, heads, skin, bones, and blood).[28] This inedible portion is increasingly being considered as a practical option to replace the use of fish meal from reduction fisheries (i.e., wild-catch specifically caught for producing fish meal) in aquafeeds.[28–30] Currently, around 20% of the global production of fish meal is supplied through the use of fishery byproducts.[9,31,32] Conversely, about 10% of the global production of fish meal is supplied through the use of aquaculture byproducts.[9,31,32] The continual growth and intensification of the aquaculture industry therefore provides an opportunity to develop the processing capacity of aquaculture to intercept additional byproducts and increase the proportion used for fish meal. This would also result in additional advantages including increasing perceived environmental sustainability of the industry, providing economic and social benefits through the valorization of waste products and creating downstream processing jobs, which will ultimately contribute to the long-term sustainability of fed aquaculture.[28]

The nutrient content of fish meal depends on the type of raw materials and manufacturing processes used in its production. In general, high-quality fish meal produced using whole fish contains 66%–74% crude protein, 8%–11% crude lipids, and <12% ash.[33] In contrast, fish meal produced from byproducts contains 52%–67% crude protein, 7%–14% crude lipids, and 12%–23% ash. For example, white fish meal produced from byproducts contains 60%–67% crude protein, 7%–11% crude lipids, and 21%–23% ash,[18,34] and tuna fish meal produced from byproducts contains 57%–60% crude protein, 8%–14% fat, and 12%–21% ash.[35–38] The lower protein content and higher ash content in byproduct fish meals are not unexpected, as the nutrient composition differs between whole fish, fillets, and other parts of the body (viscera, heads, skin, bones, and blood). The different proportions of various byproducts that are used to produce fish meal will therefore also contribute to the nutrient variability of the fish meal made from byproducts.

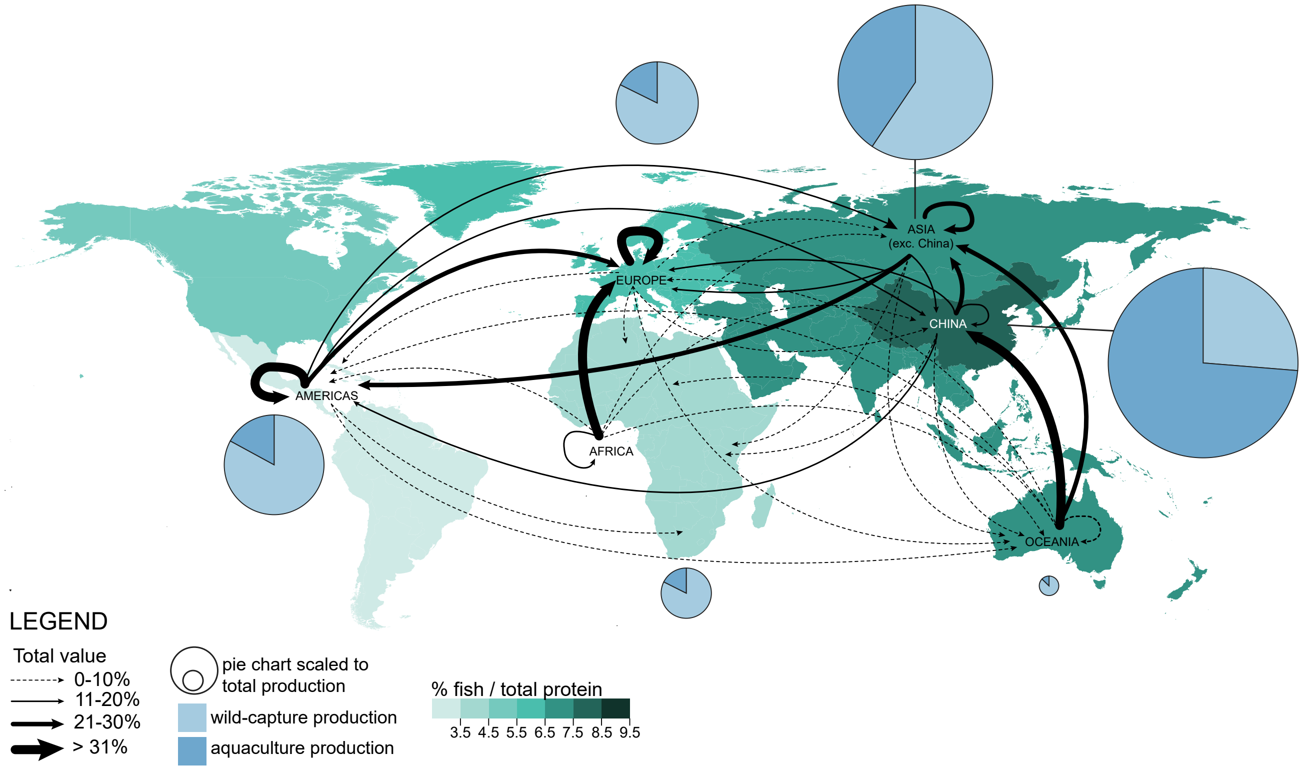


Figure 1. Aquaculture and Wild-Capture Fishery Production in Global Regions and Value of Seafood Flows
Production volume from global regions (pie charts) demonstrating the value of export flows (lines with arrows represent the percentage of the total value exported from each region), and the contribution of fish to human protein consumption (percentage of fish in total protein represented by each region's color). Data sources: aquaculture and wild-capture fishery production;[9,23] export flows;[23] and human consumption of protein from fish.[23,24]

Despite this, fish meal derived from fishery and aquaculture byproducts has been successfully used in aquafeeds, and its use is common practice in some countries.[9,12,31,32] Research on the nutritive values of byproduct fish meals has demonstrated their good potential as alternative raw materials. Fish meal from tuna byproducts can substitute 25%–30% of the protein from premium-grade fish meal without affecting the growth performance of spotted rose snapper (*Lutjanus guttatus*) when included at a rate of 15.8%–21.4%.[37] For olive flounder (*Paralichthys olivaceus*), 30% of fish meal could be substituted by tuna byproduct meal at a dietary inclusion rate of 21%.[38] For Korean rockfish (*Sebastes schlegeli*), 75% of fish meal could be substituted by tuna byproduct meal at a dietary inclusion rate of 58.1%, without compromising growth and feed utilization.[39] The less than ideal nutritional profile of byproduct fish meals presents challenges in the complete replacement of high-quality fish meal. Nevertheless, byproduct fish meal is still a viable alternative to conventional fish meal, and, more importantly, is a more economical and sustainable protein source.[39]

The industrial-scale production of fish meal and fish oil involves considerable capital investment and running costs,[19] while prolonged economic efficiency requires a constant supply of raw materials in large volumes. These factors present significant challenges when it comes to byproducts,[32,40] and it can be economically unjustifiable when raw materials need to be collected from fish-processing plants located in remote areas or when only small daily quantities are produced.[28,30,40] As such, fully benefiting from the use of byproducts will require a coordinated strategy to ensure that suitable facility infrastructures are available, that economies of scale can be achieved, and that transport networks are available—three factors that currently limit the use of aquaculture byproducts in some countries.[28] Regardless, the rising prices of fish meal and fish oil combined with positive consumer perception of byproducts will increase their viability. At present 7.5 million tons of byproducts are processed for the production of fish meal and fish oil, and it is estimated that an additional 11.7 million tons of byproducts are wasted.[32] Since capture fisheries production and aquaculture production are projected to reach 91 and 109 million tons in 2030,[9] respectively, there is enormous potential to increase the production volume of fish meal and fish oil from byproducts.

Food Waste

Food loss and food waste is estimated to be 1.3 billion tons per annum globally, accounting for 30% of all food produced.[41] According to the Food and Agriculture Organization of the United Nations (FAO),[41] food loss is defined as any food lost in the supply chain and food waste is defined as discarded food items fit for human consumption. The share of food waste in municipal solid wastes can be >50% in some larger cities.[42]

Since food wastes can be generated from various sources, their nutrient composition also varies considerably. The main nutrients in food wastes are proteins from fishmongers, carbohydrates from greengrocers, and fats from butchers, whereas the

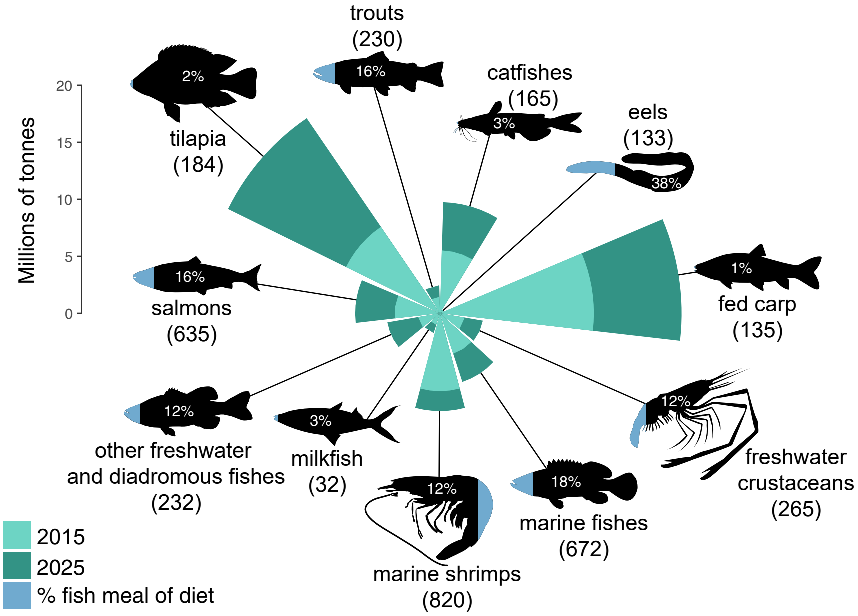


Figure 2. Projected Demand for Fish Meal in Fed-Aquaculture Diets

The estimated aquafeed volume demand (millions of tons) of the major fed-aquaculture species groups in 2015 and 2025, and the use of fish meal in the diet of each group in 2015 (represented by the blue portion of each animal). The values (percentage) inside each species group symbol are the estimated fish meal inclusion in 2015. The values in brackets beside each species group symbol are the estimated volume of fish meal included in the diets in 2015 (thousands of tons). Data sources: fish meal proportion in diets in 2015;[25] estimated aquafeed volume demand.[11]

nutrients in household and restaurant wastes are mixed.[43] The crude fat and carbohydrate content in mixed food wastes can vary between 7%–12% and 52%–68%, respectively.[44] While the crude protein level can vary from 3% to 38% depending on the type of food waste, it is possible to reduce this variation to 20%–26% by industrial processing.[44]

Food wastes have been used by some countries (e.g., China) in freshwater polyculture systems, but are not widely used within aquaculture feed pellets.[42] The growth performance of the fish is highly dependent on the species being cultured and the type of food waste being used. Pellets containing 70% sorted food waste can support adequate growth of low-trophic-level fish, including grass carp (*Ctenopharyngodon idella*), bighead carp (*Hypophthalmichthys nobilis*), and mud carp (*Cirrhinus molitorella*),[45,46] but have also resulted in reduced growth performance in grass carp.[47] Similarly, pellets with 36.5% and 73% kitchen wastes result in significantly lower weight gain in tilapia (*Oreochromis niloticus* × *Oreochromis aurea*) and giant grouper (*Epinephelus lanceolatus*), respectively, compared with fish meal controls.[48] The inclusion of kitchen waste at rates of $\leq$20% in the feed of orange-spotted grouper (*Epinephelus coioides*) can support adequate growth compared with a fish meal control diet, whereas inclusion rates of 30% or 40% results in reduced growth.[48]

There are a number of challenges when using food wastes in aquaculture feeds. Food wastes are high in moisture and are perishable, and microorganisms or pathogens may be present, which can be a health and safety concern.[42,49] Plant-based wastes can also contain anti-nutritional elements.[42] Initial waste separation can also be difficult, in terms of not only separating different types of food wastes but also separating from wastes other than food wastes, which results in high variability in nutrient composition as well as contamination. These problems can be mitigated through the sterilization of pathogens,[42,49] by using feed additives (e.g., enzymes) to enhance nutritive values, or even by improving the collection infrastructure of food waste to increase separation and traceability. Alternatively, instead of using food wastes directly, there are additional options including bioconversion and biotransformation. Bioconversion uses the food waste as a nutrient source for insects and/or algae, which can subsequently be used as a feed resource;[42,46] while biotransformation uses food waste as a nutrient source for microorganisms through solid-state fermentation[42] with the same objective (see Insects and Microbial Biomass below).

The use of food wastes in animal feed is well accepted and regulated in many Asian countries, but elsewhere there exists negative stereotypes of using waste as a feed source.[49] Regulatory barriers also exist in some countries (e.g., the European Union), and food losses rather than food wastes may be more acceptable as feed ingredients.[42,50] Although further economic analyses are required to determine the feasibility of using food losses in animal feed, it may prove suitable for lower-trophic-level freshwater fish due to their low requirements of protein and the low protein content in food wastes.

Insects

Production of insects as a protein feed input to aquafeeds does not compete with human food sources or human food production. Insects have short life cycles and can grow on a wide range of substrates with high productivity and high feed conversion factors.[51,52] Combined with relatively good nutritional profiles, the potential of insect meal as a suitable aquafeed ingredient is receiving increasing attention in many countries. The European Union approved processed animal protein from insects (i.e., insect meals) to be used in aquafeed in Regulation (EU) 2017/893 from July 2017. There are seven approved insect species, which must be raised with feed-grade substrates. Although all of these species are considered non-pathogenic, non-vectors of pathogens, and non-invasive,[53] research has mostly focused on the black soldier fly (*Hermetia illucens*), the common housefly (*Musca domestica*), and the yellow mealworm (*Tenebrio molitor*). The crude protein level in most insects ranges from 40% to 63%; however, defatted insect meal can contain up to 83% crude protein.[54] The amino acid profiles are taxon dependent and vary with species, with the Diptera group (true flies) demonstrating similar profiles to that of fish meal.[55–57] The crude lipid content of insects ranges from 8.5% to 36%, while the fatty acids profiles

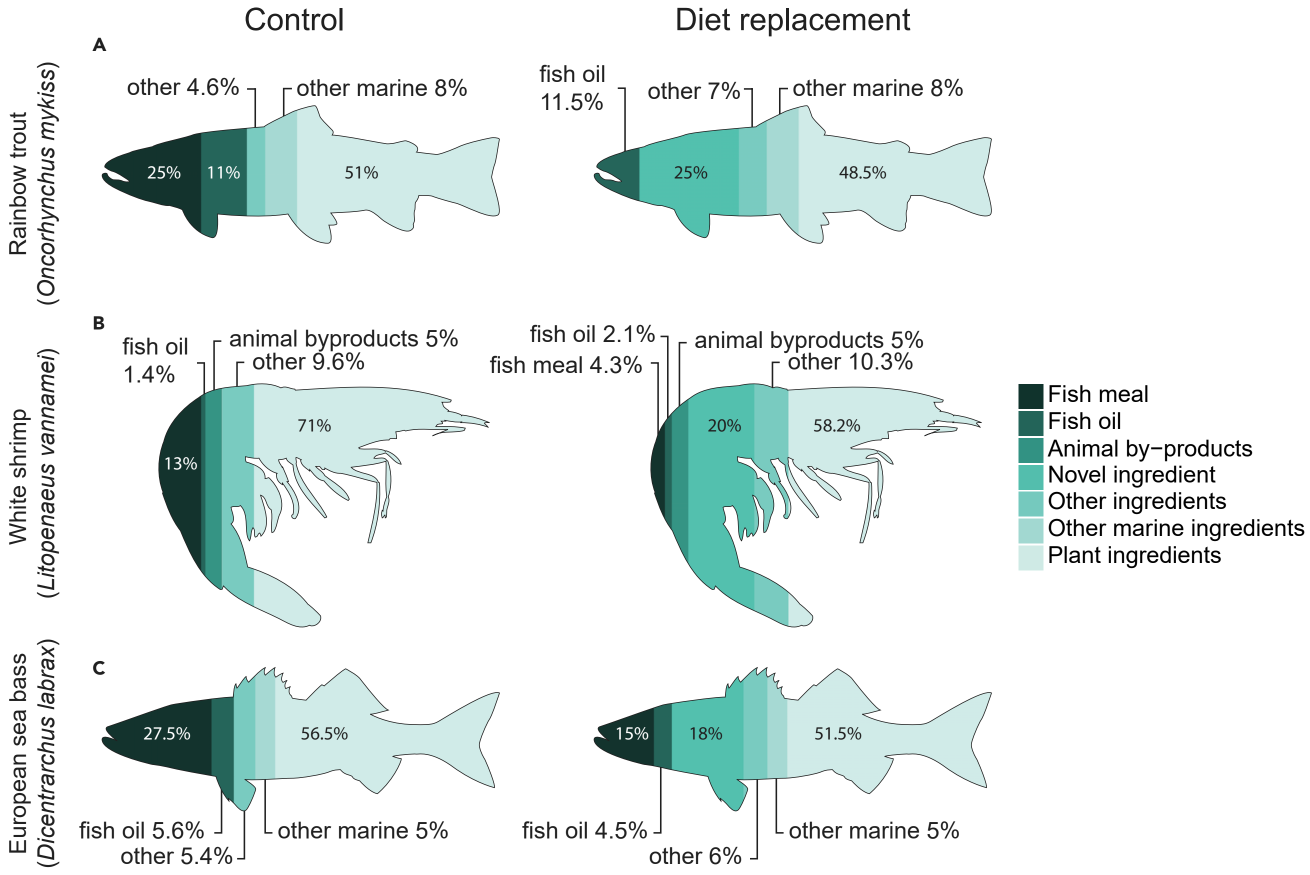


Figure 3. Case Studies of Fish Meal Replacement in the Diets for Fed-Aquaculture Species

The complete or partial replacement of fish meal using alternative protein sources demonstrated equivalent or higher growth in the animals than the control fish meal diets. Shading represents the proportion of dietary ingredients.

(A) Rainbow trout (*Oncorhynchus mykiss*) were fed a control diet with 25% fish meal or an experimental diet with 25% yellow mealworm protein meal.[61]

(B) Pacific white shrimp (*Litopenaeus vannamei*) were fed a control diet with 13% fish meal or an experimental diet with 20% microbial biomass and 4.3% fish meal.[66]

(C) European sea bass (*Dicentrarchus labrax*) were fed a control diet with 27.5% fish meal or an experimental diet with 18% freeze-dried microalgae and 15% fish meal.[67]

are variable and dependent on developmental stage and the substrates used as a nutrient source.[55,57] Insects contain negligible amounts of eicosapentaenoic acid (EPA) and docosahexaenoic acid (DHA), lower levels of omega-3, and higher levels of omega-6 fatty acids compared with fish meal. Lipid quality can be manipulated by the substrates used to raise the insects, and it is possible to enrich the EPA and DHA content by feeding insects with fish offal;[58] however, this might be economically less advantageous than feeding fish byproducts directly to fish.[57] Vitamin and mineral content are also highly dependent on substrate type.[57] Insects are low in carbohydrates (<20%), which are mostly in the form of chitin, a polymer of glucosamine[55–57] generally considered as anti-nutritional, that fish cannot digest.[59] However, there has been research demonstrating that low levels of chitin could act as an immunostimulant.[57]

Most studies that replace fish meal with insect meal recommended partial replacement (reviewed by Tran et al.[56] and Henry et al.[57]). However, an increasing number of recent studies are reporting that a 100% replacement of fish meal can be successful, even for carnivorous fish. For example, in Atlantic salmon (*Salmo salar*), insect meal produced using black soldier fly larvae replaced 100% of the fish meal at a dietary inclusion rate of 14.75%.[60] Insect meal produced using yellow mealworm at graded levels from 5% to 25% improved the growth performance of rainbow trout (*Oncorhynchus mykiss*) and achieved a 100% replacement of fish meal[61] (Figure 3A). Similar observations were made with red sea bream (*Pagrus major*) using insect meal produced using defatted yellow mealworm larvae, whereby inclusion rates of 25%–65% improved growth performance and disease resistance.[62] Conflicting results exist regarding the effects of insect meal on sensory attributes of fish fillets in the literature. Insect meal was reported to affect sensory profile of the fillets of Atlantic salmon[60] and rainbow trout,[63] but other studies did not observe any sensory differences in Atlantic salmon,[64] rainbow trout,[58] or common carp.[65]

Challenges of incorporating insect meal into aquaculture feeds include the variable and sometimes less ideal nutritional profiles.[55,56] Moreover, insect meal is currently not a price-competitive raw material for aquafeeds.[52] Economic analysis with the case of European sea bass (*Dicentrarchus labrax*) demonstrated that the incorporation of yellow mealworm into aquafeeds resulted in increased feeding costs.[68] Furthermore, production levels of insect meal are currently insufficient for constant supply,[52,68] although global production is increasing. For example, production of black soldier fly increased from 7,000 to 8,000 tons in 2014–2015 to 14,000 tons in 2016[69] and, if this continues, the price of insect meal is forecast to be competitive with that of fish meal by 2023.[69] While it will be important to scale up production to improve price competitiveness and production stability,[52] marketing strategies to brand the fish that are fed insect meals as socially and environmentally responsible could also help boost the use of insects in aquafeeds.[68]

The nutritive value of insects can be enhanced by combining insect meals with complementary nutritional profiles or by manipulating the substrate used as a nutrient source to improve fatty acid content, digestibility, and even palatability.[57] Defatting the insect source can also increase protein levels in the final insect meal produced.[57] In addition, improved resource efficiency can be achieved by using food waste as a substrate for insects and converting those waste streams into feed protein for aquaculture in countries where legislation does not prohibit such substrates. While technological improvements are required to produce a consistently high-quality product, the use of insect meal in aquafeeds has long-term potential if the price is competitive and supply can be maintained.

Microbial Biomass

The microbial biomass produced from various microorganisms, also known as ''microbial protein'' or ''single-cell protein,'' is a promising substitute for animal- or plant-derived ingredients for aquafeeds[19,70–74] (Figure 3B). Among the highly diversified group of microorganisms, bacteria, yeasts, and microalgae are generally regarded as having the highest potential for aquafeeds.[70–73] To achieve this potential there should be a focus on improving the scale of production, which will ensure the process chain is environmentally sustainable and reduce the cost of production.[70–72]

Bacteria and yeasts have a relatively high protein content (50%–65% and 45%–55%, respectively), with amino acid profiles that are comparable with fish meal[70,72,73] and can potentially be used as either functional feed additives or as alternative raw materials.[70,72–77] The nutritional profile of bacteria and yeasts can also be manipulated or enhanced by modifying the culture media, growth conditions, and post-harvest treatments.[70,72] The resulting microbial biomass produced can provide excellent nutritional characteristics for aquatic animals.[70,72–77] For example, yeasts derived from hydrolyzed lignocellulosic biomass through fermentation are a suitable source of protein for the diets of fishes, including carnivorous species such as Atlantic salmon and rainbow trout, with the caveat that additional synthetic methionine would have to be supplemented in the feed.[72] There is also a range of commercial products available in the marketplace[70,72,74], including Novacq, a potent microbial bioactive that can reduce the quantity of fish meal required in the feed of the black tiger prawn (*Penaeus monodon*) while maintaining growth rates.[75] However, even though bacteria and yeasts have high potential as an alternative source of protein for aquafeeds, their use is still limited due to the high cost of production.[73] Their suitability and inclusion rates will also need to be evaluated at the species level, with a focus on their digestibility and the bioavailability of nutrients contained within the microbial biomass.[70,72,73,75,76]

Microalgae are cultivated and used as a feed resource in the aquaculture industry and are invaluable during the larval rearing stage of many aquaculture species.[77] The nutritional quality of microalgae is high, with a crude protein content of up to 71% and a lipid content of up to 40%, which are comparable with that of terrestrial plant and animal sources.[78–80] Microalgae have the potential to replace fish meal and fish oil in aquafeeds[71,77,81] and many studies have demonstrated the successful use of microalgal biomass as a feed additive or fish meal replacement for a range of aquaculture species, generally with positive effects on growth and quality[70,81–87] (Figure 3C). The biological capacity of microalgae, underpinned with positive research findings on the replacement efficacy in aquafeeds across many aquaculture species, suggests that there is high potential for the use of microalgae as a protein source. However, this potential is diminished by the technical, biological, and economic difficulties regarding the continuous production of high-quality microalgal biomass, and its downstream processing, at scale.[40,79,88–90] The current world production of microalgae (auto- and heterotrophic) is estimated to be approximately 40,000 tons per year,[90] only 0.7% of what would actually be needed to replace the protein from fish meal in aquaculture. In addition, the current price of microalgae is between US$10 and $30 per kg, several magnitudes higher than soybean meal ($0.30 per kg), hence global production is limited to high-value niches in the human supplement and nutraceutical markets.[19,90–92] Although attempts have been made to model the cost and production of microalgae to satisfy the protein demand of aquaculture,[93–95] such efforts can only be considered as academic exercises as they do not take into account the difficulties of upscaling production from medium scale (<1 hectare) to large scale (>10,000 hectare). Therefore, due to the current low volumes, high production costs, and cultivation challenges, it is highly unlikely that microalgae will become a viable alternative source of protein for aquafeeds in the next decade.

Macroalgae

The production of marine macroalgae (also termed seaweeds) is an established industry that accounts for nearly 30% of global aquaculture production, with an output volume of 30 million tons per year that is worth more than $6 billion.[96] Nearly 90% of all cultivated seaweeds are produced in China and Indonesia.[9,96] The main species of seaweed, which account for 95% of the total production, are *Eucheuma* spp., *Laminaria japonica* (Japanese kelp), *Gracilaria* spp., *Undaria pinnatifida* (Japanese wakame), *Kappaphycus alvarezii*, and *Porphyra* spp. (Japanese *nori*),[9,96,97] the majority of which are produced almost exclusively for human consumption.[9,96,98] In addition to targeting high-value applications, recent developments have demonstrated the bioremediation capacity of both seaweeds and freshwater macroalgae, and their integration into existing sources of nutrient-rich waste water from agriculture, aquaculture, municipal wastewater treatment, and power generation.[99–104] The key to this concept is that, as these macroalgae grow they assimilate dissolved nutrients (particularly inorganic nitrogen and phosphorous), which would otherwise be wasted, from the water column and convert them into biomass and, consequently, a source of protein. This provides a unique opportunity to recover waste nutrients, allowing these industries to expand and intensify production while minimizing their environmental impact. The potential scale of this resource is impressive, with a demonstrated biomass production rate of 45–70 tons of dry weight hectare^{-1} per year and an average crude protein content of ~22%.[103,105]

The proportion of crude protein in macroalgae, particularly when harvested from the wild, is highly variable, ranging from <1% to 48% of the biomass dry weight,[99,106–109] and depends on both species and environmental conditions. It should be noted that many of the crude protein values reported in the literature are overestimated,[110] and the true crude protein content, representing a more realistic range, is 10%–30% when grown under non-limiting nutrient conditions.[111–113] Despite this, macroalgae are considered to be a high-quality source of protein, with the majority of species having equivalent, or higher, total essential amino acids as a proportion of total amino acids than traditional agricultural crops and fish meal.[99,113–115] For example, one of the first limiting amino acids in plant-based diets of fish and crustaceans is methionine,[116] which makes up a higher proportion of the total amino acids in macroalgae compared with soybean meal and can be up to twice as high.[99,110,114] In contrast, the absolute concentration of essential amino acids on a whole biomass basis is substantially lower in macroalgae (5.5% dry weight) than in soybean meal (22.3% dry weight) and fish meal (31.2% dry weight),[113] due to high concentrations of complex polysaccharides (up to 76% dry weight),[117] also known as dietary fiber. Dietary fiber limits the digestibility of the algal protein fractions and affects the overall nutritional value when incorporated into aquafeeds.[118–120] Accordingly, inclusion levels of macroalgae at rates >10% generally have negative effects on growth and feed conversion of commercial fish species.[121–124] However, macroalgae is still suitable when incorporated as a functional feed ingredient at low levels and, when included at rates <10%, there are often positive effects on the animals being cultivated.[122,125,126] The bioactive compounds found in macroalgae are associated with health-promoting effects including improved stress resistance and enhanced immune function.[127–131] In addition, macroalgae enhance the flavor of farmed fish[132,133] and act as a feeding stimulant, which indirectly boosts protein intake.[127,134,135] As such, using whole macroalgal biomass as a functional feed additive for aquatic animals is a promising application.

Using whole macroalgal biomass as an alternative protein source has been successful in conjunction with herbivorous aquatic animal species.[136–140] This has been particularly successful for abalone, whereby seaweeds are cultivated in the discharge water and then used as feed.[100] There is also potential for its use with omnivorous species,[141] as these animals have lower protein requirements compared with carnivorous fish.[142] Currently, the opportunity and value of using macroalgae in aquafeed for carnivorous fish lies more in its application as a functional feed ingredient to improve the health and welfare of these animals rather than as a viable large-scale alternative protein source. If macroalgae are to replace fish meal in aquafeeds, processing of the biomass is required to deliver a more concentrated form of the protein. This can be achieved either through the direct extraction and isolation of protein or by removing non-protein components, such as ash and soluble carbohydrates, thus increasing the relative proportion of protein in the residual macroalgal biomass.[105,143–146] However, these processes are still being developed and while not yet commercialized,[145] they have been successfully applied to *Ulva ohnoi*, a commercially grown bioremediation species, to increase its protein content from 22% to 45% on a dry-weight basis.[105] Importantly, the quality of the concentrated protein in that study was comparable with that of soybean meal and white fish meal, suggesting that it would be a suitable protein replacement option, with the caveat that it still must be tested *in vivo*.[105] Although this process is currently in its infancy, the development of macroalgae as a source of protein will provide a net increase to the supply of protein for the world. Macroalgae cultivated through bioremediation represents an environmentally friendly alternative to many traditional sources of protein and will help to alleviate some of the competition for protein resources between aquaculture and terrestrial livestock production.

Improvements in Efficiency

Improving animal performance and animal health is a key to not only reducing aquaculture production costs but also reducing environmental impacts including decreasing carbon footprints.[147,148] Traditionally, in aquaculture to date, this has been implemented through the optimization of feed formulations to achieve the most efficient feed conversion ratios (FCRs), which represent the quantity of feed consumed to produce one unit of animal biomass gain. The optimization of FCRs is based on maximizing animal survival and growth traits.[148] However, for species that require relatively large quantities of fish meal and fish oil in their diets, this can be environmentally and economically unsustainable given the limited fishery resources.[149,150] A sustainable solution would be for farmed animals to be fed renewable plant-sourced and emerging alternative protein and oil products, while at the same time improving FCRs and other production traits through husbandry, species-specific feed formulation, functional feed additives, and selective breeding practices and their interaction (i.e., genotype × diet interaction).[148,151] Consequently, there is considerable scope for improved efficiency in fed-aquaculture production.

The transition toward plant-based diets has been challenging, and the effects of plant ingredients on animal growth and health have been widely studied.[152–154] Plant-based diets typically contain carbohydrates that have low digestibility in carnivorous animals as well as anti-nutritional elements that affect feed intake, feed efficiency, metabolism, and health.[155,156] While many aquaculture species are carnivorous (e.g., salmon and tuna), others are omnivorous or herbivorous (e.g., shrimp, tilapia, catfish, and carp species); therefore, different species vary in their capacity to effectively use different kinds of animal or plant feed ingredients. Recently, feed formulations have improved, allowing complete substitution of animal-based diets with plant-based ones in some species.[157] However, these results are species specific, and total substitution with plant-based ingredients can still negatively affect survival and growth rates in other species.[158] Based on modern advances in feed ingredient processing and gene technology, there is now the capability to process and/or engineer plant crops as feed ingredients that specifically address the challenges of incorporating plant-based products into aquafeeds.[159,160]

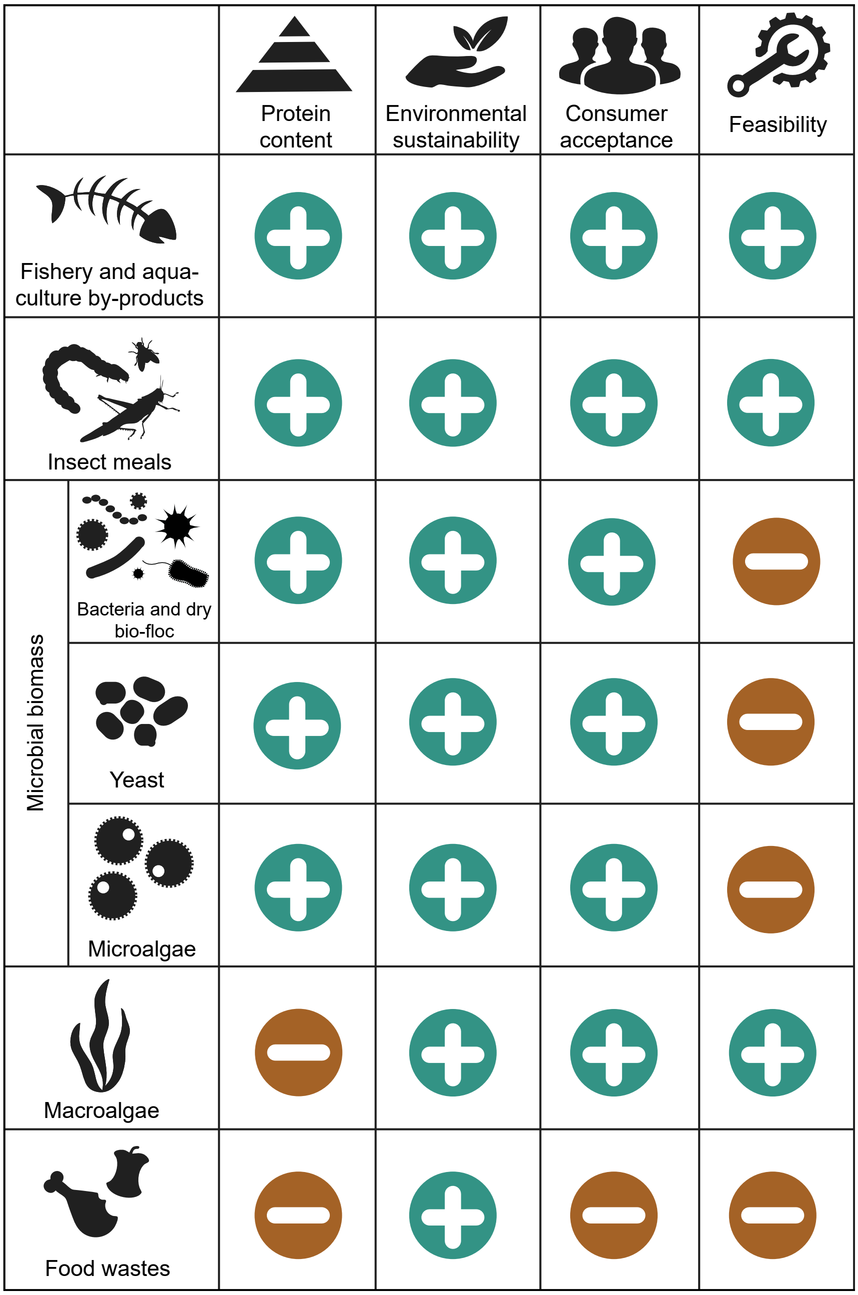
At present, soybean meal is a primary source of vegetable protein in aquafeeds.[156] In an attempt to negate the negative effects of soybean inclusion, biotechnology (i.e., gene expression and silencing) is being used to suppress anti-nutritional elements or to alter seed protein composition for increased digestibility.[159–161] In addition, biotechnology can be used to value-add by genetically modifying soybean to produce unique products for specific animal requirements. For example, soybean with higher proportions of omega-3 fatty acids can be used for enhanced animal growth and human health benefits,[89,162] and soybean with carotenoid gene enhancements can be used to enhance the flesh pigment of salmon.[161,163] There is also research demonstrating the use of prototype vaccines engineered by plant biotechnology for inclusion in plant-based aquafeeds for species requiring mass oral immunization.[161,164]

In addition to the modification of soybean, there has been an emergence of functional feed additives in aquaculture diets.[75,165–167] Functional feed additives can indirectly act as growth promoters by improving immune function, reducing oxidative stress, and enhancing disease resistance, rather than directly providing extra nutrients essential to growth. There is an array of products sold under commercial trademarks (e.g., Novacq, ALIMET, and Sanocare) that report improved survival and growth,[168–171] and while the active ingredients of these can include bioactives obtained from plant-derived purifications, the majority appear to be from microbial biomass-derived sources. In the absence of recombinant engineering of microbes, most of the processes used to produce functional feed additives are discoveries of biological action and lack the enforceable protections of a patent (e.g., US H2218H). Consequently, there is a high level of commercial secrecy around their production and mode of action. After reviewing a number of patents that exist relating to microbial biomass products, it is apparent that their mode of action is through immune stimulation, gut microbial/microbiome modulation, or improved expressers of nutrient elements including selenium (Patent EP1602716A1), glucosamine (Patent US H2218H), and essential fatty acids (Patents JP599652B2 and US6255505B1). Considering that the majority of functional feeds promote immune response and growth, it is perhaps misleading to consider them ‘‘optional additives’’ within the context of aquafeed preparation. Rather, they could be considered as additives that ameliorate deficiencies in current diet formulations. Recognizing that aquafeeds must supply the full spectrum of nutritional factors to support the action of multiple biological pathways within an animal (including immune competence under typical culture conditions) will facilitate a more logical and systematic approach toward the replacement of fish meal.

Many studies have sought to improve diet formulations, whereas others have focused on improving the performance of the animals fed a variety of diets through genetic improvement programs.[147,151] Several studies have demonstrated the existence of genetic variability in different wild stocks as well as domesticated animals fed different proportions of fish meal and, therefore, protein. For example, divergent wild stocks (i.e., discrete genetic pools) of the freshwater prawn (*Macrobrachium rosenbergii*),[172] alternative genetic strains of tilapia (*Oreochromis* spp.),[173] and selected groups of black tiger shrimp (*Penaeus monodon*)[174] have different capacities to use different animal proteins. Furthermore, the mean heritability (h^2) estimates for feed efficiency traits (FCR and reduced residual feed intake [RFI]) in farmed fish range from 0.07 to 0.47, providing support for genetic improvement through selective breeding programs.[148,175] In these studies, rainbow trout (*Oncorhynchus mykiss*; h^2 FCR 0.12; h^2 RFI 0.13–0.23)[175,176], sea bass (h^2 FCR 0.23 pedigree and 0.47 genomic),[177] European whitefish (*Coregonus lavaretus*; h^2 FCR 0.07),[178] and Nile tilapia (*Oreochromis niloticus*; h^2 FCR 0.32)[179] had moderate heritability estimates sometimes comparable with terrestrial animals (h^2 range of 0.12–0.67).[179–181]

While heritability estimates for feed efficiency are starting to emerge for farmed fish species, the lack of comprehensive heritability measurements among other aquatic animals is partly due to the difficulty in obtaining accurate trait measurements.[182] Although the concept of measuring aquaculture feed efficiency for selective breeding is long-standing, it lags behind terrestrial animal production, as recording feed intake routinely in individual animals in commercial aquatic systems is a considerable challenge.[176,182] Therefore, feed efficiency improvement using phenotypic trait selection in aquaculture can be difficult. The development of genomic approaches such as ‘‘genomic selection’’ can increase the precision of estimated breeding values for feed efficiency traits, which can then be used in selective breeding programs.[183] In this approach, large numbers of genome-wide genetic markers aid in animal selection. Here, most quantitative trait loci (QTL) regulating feed efficiency will be in strong linkage disequilibrium with at least one genomic marker. As such, genomic selection methodology simultaneously estimates the combined genetic effects of all relevant QTL and provides accurate predictions of genetic merit for an animal.[184]

Of particular interest is the selective breeding of aquaculture animals that can effectively use plant-based ingredients without negative side effects. For example, there is significant genetic variability around growth traits of rainbow trout (*Oncorhynchus mykiss*) when provided a plant-based diet (including high heritability estimates for body weight; e.g., 0.43–0.69),[185] suggesting that genetic progress is achievable.[185–187] Furthermore, additional studies have demonstrated genetic improvement in growth traits by selectively breeding animals on a plant-based diet (e.g., rainbow trout[157] and salmon[188]). However, when transitioning production animals from conventional feed ingredients to plant-based diets, the interaction of genetics and diet (i.e., reranking of family performance on specific diets) needs to be considered, particularly in established breeding programs. Significant genotype (animal performance) by diet (plant-based diets) interactions have been observed in fish whereby some animals can more effectively accept and use the diets than others.[189,190] It is apparent that animals that performed well on traditional animal-based diets may not necessarily perform equally well on a plant-based or modified diet. However, exposing fish to plant-based diets early in life improves later-life fish performance when fed the same diet again.[191,192] Regardless, to ensure optimum genetic gain and productivity, the aquaculture industry needs to develop selective breeding programs specific to plant-based diets from first feeding.



		Protein content	Environmental sustainability	Consumer acceptance	Feasibility
Fishery and aquaculture by-products		+	+	+	+
Insect meals		+	+	+	+
Microbial biomass	Bacteria and dry bio-floc	+	+	+	−
	Yeast	+	+	+	−
	Microalgae	+	+	+	−
Macroalgae		−	+	+	+
Food wastes		−	+	−	−

Figure 4. Qualitative Feasibility Assessment of Alternative Protein Sources for Fed-Aquaculture Diets

The broad-level qualitative assessments of alternative protein sources were based on a combination of the current-day realities and the future potential (10–20 years) of each protein source. Positive (+) represents a protein source with high potential to meet demand, while negative (–) represents a protein source that has obstacles that will need to be overcome before development. The assessments were subjective and based on a relative comparison with fish meal from wild-capture fisheries (for proximate composition see Figure S1). The assessment for "feasibility" was determined by considering the economics of commercial-scale production, the relative limit of the resource, the likelihood of meeting consistent supply, the short-term prediction of commodity price, and the legal ease of implementation.

Future Directions

Feeds for lower-trophic-level freshwater fish species (e.g., catfish, tilapia, and herbivorous carp) contain considerably lower levels of fish meal compared with those for carnivorous species (e.g., salmon, other marine fishes, diadromous fishes, eels, and marine shrimps; Figure 2). Therefore, consumer awareness, labeling, and interest in seafood sustainability may help increase consumption rates of farmed freshwater fish at the expense of species with greater protein demands. As a caveat, to date there is limited evidence for an increase in consumer demand for sustainable seafood as a result of sustainable seafood labeling.[193]

Although the percentage inclusion level of fish meal in feeds is low for farmed freshwater fish in comparison with marine fish and crustaceans, the global production of these fed carp, catfish, and tilapia is very high[11] (Figure 2). Therefore, the inclusion of even low levels of fish meal results in substantial quantities of fish meal overall. Given the projected increase in production of these species and associated aquafeed demand (Figure 2), substituting fish meal by alternative protein sources in these diets will result in a considerable reduction in the total quantity of fish meal used. Simulations by Froehlich et al.[12] suggest that this sector has the highest potential to mitigate the use of forage fish by mid-century.

Significant gains in aquaculture production to supply additional protein, especially for freshwater fish, may also be made by combining unfed aquaculture with fed aquaculture or through the development, promotion, and expansion of polyculture-based systems, resulting in the simultaneous culture of multiple fed species in a single system.[194] In the related integrated multi-trophic aquaculture systems, which combine fed aquaculture with extractive aquaculture, a higher yield of protein is achieved through the production of several products.[100,101,195] While detailed knowledge is required to balance multiple species,[196] these systems have the added benefits of nutrient bioremediation and positive consumer perception.

The greatest challenges to alternative protein sources in aquafeeds include variable protein content (see Figure S1) and the feasibility of increasing production, which is a function of available processing technologies, cost, and scalability (Figure 4 includes a subjective assessment of ingredient potential). Consumer acceptance also varies among these raw materials. Given these challenges, there is enormous potential for technological improvements to consistently produce high-quality alternative protein products with enhanced nutritional profiles, while economies of scale can result in improved price competitiveness. Some protein sources, such as fish byproducts and insect meals, are viable and promising alternatives to conventional fish meal, whereas some raw materials such as food waste may still need to overcome a number of obstacles before becoming a staple in formulated aquafeeds (Figure 4) and may find greater use in bioconversion/biotransformation.

It is important to bear in mind that aquaculture feeds are formulated using a multitude of ingredients and it is unlikely, nor necessary, that a single protein source will meet the requirements of the cultured species or fully replace fish meal. Multiple protein sources can also be used in combination to benefit from their complementary nutritional profiles. Feed supplements can also be used to balance the nutrient composition of the feeds and functional ingredients can be used to facilitate the replacement of fish meal with alternative ingredients. Furthermore, using multiple protein sources allows flexibility in feed formulations when ingredient prices fluctuate,[192] as feed manufacturers often use cost as a determinant in selecting ingredients.

There has been a 4-fold increase in fed-aquaculture production from 12.2 million tons to 50.7 million tons from 1995 to 2015.[197] In parallel, the increase in aquafeed production was 6-fold, from 7.6 million tons to 47.7 million tons from 1995 to 2015.[25,197] Even though aquafeeds only account for a small proportion (less than 4%) of total global animal feed production, the ingredients used are also used in terrestrial livestock feed, pet food, and human food.[11,25,192] Therefore, developing and optimizing alternative sources of protein for aquafeeds will play an important role in ensuring a socially and environmentally sustainable future for the aquaculture industry.

SUPPLEMENTAL INFORMATION

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