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REVIEW ARTICLE

Harvesting the benefits of nutritional research to address global challenges in the 21st century

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Abstract

Over the past 20 years, substantial progress has been made in improving feeds and feeding technologies for most aquaculture species. Notable improvements in feed conversion efficiency (through a better understanding of requirements and improved feed management) and ingredient sustainability (through increased capability to use a wider range of ingredients) have been achieved. While advances have been made in understanding the requirements of many of the main aquaculture species, there is still much to be done in defining requirements, especially for many of the species being farmed in the developing world. Gains in the efficiency of feeds are slowing for developed species, but potential gains are still appreciable for less developed species. There is a growing need to more precisely prescribe the required levels of essential nutrients and various additives in the diet based on age, genotype, environment, and immune status to deliver a “precision nutrition” approach to farming aquaculture species. There is still further need to diversify our ingredient options to provide greater

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resilience, as the sustainability of different feed ingredient sources, including possible climate change impacts, is becoming a growing issue. There is a growing demand for biocircularity in our feed ingredient supply chains. Ultimately, what is needed to sustain future feed ingredient needs are sustainable sources of cost-effective protein, some essential amino acid additives, some omega-3 fatty acid resources, and various minerals and vitamin additives. The increasing use of new and varied resources will ensure that food safety remains an important issue throughout the world. Feed manufacturing has evolved from a simplistic exercise to a highly complex science with state-of-the-art engineering, but its application is not consistent across all sectors, as there is still widespread use of pelleting, mash, and trash fish feeding in the developing world. Similarly, feed management has also dichotomized between the developed and developing world, with a high reliance on manual skilled labor in the developing world, whereas more advanced aquaculture systems are becoming increasingly reliant on automated computer-controlled feeding systems.

KEYWORDS
aquafeed, feed conversion efficiency, nutrition, sustainability

1 | INTRODUCTION

With any science-based prediction of the future and of which path to follow (essentially a navigation exercise), we need to understand where we are and where we have been. It is only once we understand this context of our situation that we can then begin to make some rational prediction about where we are heading. As such, in this article, we examine the three key themes that underpin the feeds and feeding process (requirements/ingredients/management) and have framed our review of this journey in terms of the past–present–future. Additionally, it needs to be noted that the top seven cultured species groups (carps, tilapia, catfish, shrimp, other freshwater fish spp., salmonids, and other marine fish spp.) collectively comprise close to 90% of all aquaculture production and as such form the focus of the article. While increasingly, each of these species' groups is being produced intensively and are reliant on compounded feed for their sole nutritional inputs, this is not equally the case among all seven groups. Substantial production, particularly of carps, which comprise almost 50% of global aquaculture production, are still produced in small-scale extensive, semi-intensive, and integrated polyculture systems with little to no manufactured feed inputs. Notably, feed specifications, ingredient use, and feeding practices also vary regionally across the world. As such, in this article, we have attempted to generalize on those issues that affect the three key themes that underpin the feeds and feeding process across the world.

2 | REQUIREMENTS

2.1 | Past (prior to 2010)

The terms nutrient "requirement" and "specification" have frequently been used interchangeably. While "specification" is the detailing of the design instructions for something (e.g., a diet containing 40% protein), the actual nutrient requirement of an animal is more based around the need for a particular nutrient required at a certain metabolic body weight and for a defined duration (e.g., mg protein/$kg^{0.7}$/d), and for defined physiological functions such as maintenance, maximal growth, or optimal health. The process of establishing these nutritional requirements (optimum dietary levels) for aquaculture species has been a big challenge not only because of difficulties associated with feeding an aquatic animal but also because of considering the increasing number of species of commercial importance (Boyd et al., 2020; Hua et al., 2019). This contrasts with what has happened with terrestrial domestic species, such as poultry and pigs, where the definition of nutritional requirements is generally focused on a single species, and has varying recommendations based on production stage and/or objective (e.g., broilers or layers in poultry) (NRC, 1981). Additionally, finfish and shellfish requirements can vary not only among species but also on their developmental stage and in some cases different environmental constraints (NRC, 2011). Moreover, requirements may further depend on the farming system used and regionality. In many cases, production of key aquaculture species was and still is undertaken in extensive, semi-intensive, and integrated polyculture systems, meaning that a holistic systems approach to nutrition had to be used rather than a monoculture approach. Aquaculture was notable in being much more varied in the nutritional requirements of its species than those in livestock production.

Traditionally the definition of requirements for essential nutrients (energy, protein, lipid, amino acids, fatty acids, vitamins, and minerals) for most species was undertaken on a gross nutrient basis only (Boonyaratpalin, 1997; Cowey, 1992; NRC, 2011). Requirements were typically defined based on empirical experiments and limited to young animals and laboratory environments. This served well in terms of defining the distinct differences among many of the species and between aquatic and terrestrial animals (NRC, 2011).

Initially, the definition of nutrient requirements for many species led to big gains in feed efficiency, with improvements in FCR values from 1.8–3 to 1.2–1.8 being achieved for many species (Hua et al., 2019; Boyd et al., 2020; Tacon, 2020; Naylor et al., 2021; Hardy et al., 2021). However, as time has passed, there have been diminishing returns on any improvements in the definition of nutrient requirements across most species' groups (Figure 1).

The use of various modeling systems in aquaculture to define requirements for energy and some macronutrients and explore various physiological processes was established prior to 2010 (Dumas et al., 2010; Shearer, 1995). These models were largely derived from similar approaches used for terrestrial species but had to include various empirically derived features to account for the differences between ectotherms and endotherms (Cho & Bureau, 1998; Lupatsch et al., 2001). Different iterations of either nutrient flow or nutrient demand models were developed, which were largely based around factorial bioenergetic processes (Cho & Bureau, 1998; Glencross, 2008; Han et al., 2011).

2.2 | Current status (2010–2020)

Since 2010, smaller improvements in feed efficiency have been made, with typical changes from FCRs of 1.5–2 to 1–1.5 for some species (Figure 1). Such gains were mainly because of the increasing knowledge about nutritional requirements but also because of better management practices following the intensification of growing systems (NRC, 2011). An increasing level of replacement of fish meal with plant proteins as the main ingredients in commercial feeds demanded a better knowledge of amino acid requirements. Although fish meal has an amino acid balance close to that of many fish requirements most plant proteins do not, thus meeting fish demands for growth with plant

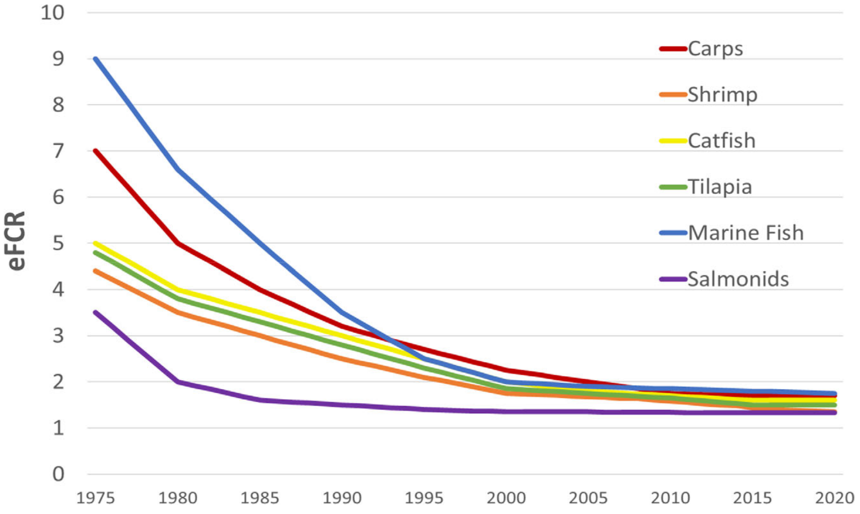

FIGURE 1 Changes in economic feed conversion ratios (eFCR) of major aquaculture species groups over the past 45 years.

proteins required a deeper knowledge of amino acid requirements in terms of amounts and balance (Kaushik & Seiliez, 2010).

This was especially important for carnivorous species, which have higher demand for amino acids, but it was also important for omnivores such as tilapia and shrimp, where the high cost of fish meal limited its use in commercial feeds. A deeper knowledge about the requirement of other nutrients such as taurine, n-3 fatty acids, and various vitamins and minerals also became important with increasing levels of fish meal replacement, as these nutrients are less available or even absent in plant sources (Domínguez, Montero, et al., 2020; Domínguez, Sehnine, et al., 2020; Gatlin III et al., 2007).

During the 2010–2020 decade, after the key NRC publication (NRC, 2011), there was an increasing level of definition of requirements for animals of different sizes and in some cases different environmental constraints (e.g., hypoxia, temperature, salinity, etc.). Both age and environmental conditions may markedly affect fish physiology and modulate the expression of key genes, affecting nutrient utilization and nutritional requirements (Fernández-Palacios et al., 2011; Hamre et al., 2013; Izquierdo & Koven, 2011; Lund et al., 2019; Torno et al., 2019). However, such information is still scattered or absent for some species (e.g., *Seriola*, Sole) (Sicuro & Luzzana, 2016; Valente et al., 2019). Industrial breeding programs are rapidly progressing for a few species, based on recently developed customized genomic tools for marker-assisted selection, and are producing fast-growing animals with improved FCR that may have different requirements for specific nutrients (Glencross et al., 2013; De Verdal et al., 2018; Lee et al., 2020; Ferosekhan et al., 2021). Moreover, nutritional history (protonutrition) and nutritional programming affect the utilization of dietary nutrients and therefore could affect fish requirements (Turkmen et al., 2019). The main drivers for such development were the high cost of aquafeed, which typically represents 50% of the variable production cost of intensive aquaculture, together with the increasing pressure for producing more sustainable diets able to address the Sustainable Development Goals established by UN. This implies knowing more about the requirements of the various species to sustain optimal growth and produce high quality and healthy animals. In many of those species already produced at large scale, requirements for macronutrients and most micronutrients are now well established for early/larval, juvenile, grower, and brood stock stages of the production cycle. But most non-mainstream species still need clearer definition of many of the basic nutrient requirements and their response to environmental constraints remains largely unknown. Modern aquaculture uses diets that rely on a variety of alternative raw materials that need to be balanced with additives including certain amino acids, minerals, and vitamins to ensure the optimal use of the feed. However, to face various growing environmental and production challenges, the currently established requirements of many amino acids and other micronutrients may need to be revisited to assure fish growth and robustness into the future (Aas et al., 2019; Berntssen et al., 2018; Hamre et al., 2016; Kousoulaki et al., 2021; Prabhu et al., 2014).

The last comprehensive compilation of nutritional requirements of fish and shrimp was published in 2011 (NRC, 2011), although a recent revision of the "Fish Nutrition" book by Hardy et al. (2021) has been timely. This publication included the requirements of various freshwater and marine fish as well as shrimp of commercial importance. Despite organizing and facilitating access to nutritional requirement information for various important aquaculture species, it also made clear several unknowns not only on micronutrient (vitamins and minerals) but also on amino acid requirements. Notably, the compiled requirement specifications were largely defined from animals in juvenile stages and based on using highly digestible diets and animals maintained in optimal growing conditions. In most cases, requirements were presented as a single recommendation for each species and did not consider changes in requirements throughout the various production stages or production systems. Therefore, despite the increasing use of farming system environments to undertake research and provide industrially relevant information for some species such as salmon, this is not so for many other species (Ng & Romano, 2013).

Most feeds in the world are still formulated on a crude composition basis, although there is increasing formulation of feeds on a digestible nutrient basis in the developed world for some species such as Atlantic salmon. The quality of the formulation depends on various knowledge sets, including the accurate understanding of the nutrient requirements, the nutritional composition of the ingredient being used and their nutrient digestibility and/or bioavailability, and the processes being used to form the feed into a physical pellet. While the feed of salmon is formulated to be highly efficient, the feed efficiency of most other cultured fishes or shrimp lags that of salmon.

This is mainly because of the rapid development of aquaculture with high diversity and complexity of cultured species and feed ingredients used in developing countries, and the lack of comprehensive knowledge of essential nutrient requirements of so many cultured animals and of the digestibility or the bioavailability of nontraditional ingredients or their nutrients. For example, nutritional studies published in China have been conducted on more than 200 species, representing a wide geographic distribution, different feeding habits (herbivorous, carnivorous, omnivorous, and filter feeders), and different culture modes. It is evident from the information provided in the NRC (, 2011) that the tables listing the nutritional requirements of salmonids are mostly complete, while those for many other important marine or freshwater species are either incomplete or mostly blank (Hardy et al., 2021). Despite the almost 700 species produced in aquaculture, increasing pressure in the last decade for further species diversification has brought attention to several either low trophic species or very fast-growing or endangered species (Boyd et al., 2020; Cottrell et al., 2021; Naylor et al., 2021; Newton et al., 2021).

Over the past decade, there has been a growing use of factorial and nutrient-flow (or demand) modeling systems to define requirements for energy and macronutrients for an increasing number of species. Such models are now being widely used to iteratively define nutritional requirements for various species across their production size ranges and within varying environmental conditions (Chowdhury et al., 2013; Glencross & Bermudes, 2012). There have been increasing levels of adoption of modeling by the commercial aquaculture sector as a means of refining feed design and improving feed management. Furthermore, the development of mechanistic models has further advanced our understanding of the interrelationships between different metabolic pathways and nutrient use and how this influences growth and body composition (Bar et al., 2007; Bar & Radde, 2009).

A growing understanding of the role of the microbiome in nutrient supply/utilization has emerged. Brought about by low-cost methods to evaluate microbial diversity using 16 S ribosomal RNA sequencing technologies, this has enabled an increased understanding of the physiological interaction between the microbiome and its host. However, its potential to mediate how organisms respond to multiple environmental factors remains poorly understood. For example, most aquafeeds contain carbohydrate-based binders (e.g., starches), which do not exist in the aquatic environment. These complex carbohydrates are influential in the development of particular microbiomes. Differences in microbiome structures have been observed between fish fed either extruded or nonextruded pellets containing starch (Barreto-Curiel et al., 2018). So, it is apparent that the gelatinization process is influential to the structure of the different microbial communities. Understanding the impacts of such dietary changes on the resulting microbial communities will be helpful to identify those strategies that are beneficial or not, so long as the feed is included as a control element (Fuentes-Quesada et al., 2018; Karlsen et al., 2022). Another important aspect is the differences in microbiome structures in organisms subjected to stress, whether because of effects of system intensity, environmental contamination, temperature, and/or nutritional deficiencies. Studies have shown that stress, particularly chronic stress, and microbial manipulation (probiotics or prebiotics) influence the microbiome structure of the fish gut (Anker-Ladefoged et al., 2021; Rimoldi et al., 2020; Serradell et al., 2020). However, there is still insufficient information on the influence of nutritional, environmental, or genetic factors on the microbiome on fish growth and health to assess the economic benefits of adding probiotics in the feed or water.

The growing need for immune-enhancing diets comes back to issues of poor definition of micronutrient supply under prevailing conditions linked to large-scale marine ingredient replacement without tacking all the required issues comprehensively. Consequently, functional feeds are being developed to enhance animal health. Such functional feeds must have optimized nutrient composition and are supplemented with some functional additives, allowing the farmer to not only meet the needs for better growth but also improve the immunity, stress resistance, and health status of aquaculture animals, while ensuring the quality and safety of the products.

The most common functional additives used in aquafeeds include preservatives (antioxidant), nutritional supplements (amino acids, vitamins, and trace elements), enzymes, pigments (carotenoids), palatants, and immunomodulators (probiotics, prebiotics, plant extracts, and nucleotides). The mechanistic action of such functional additives is multidimensional. They can act directly and/or indirectly on the animal, such as antioxidation, modification of gut microbe profiles, improvement of digestive tract morphology, elevation of digestive enzyme activities and nutrient absorption, and enhancement of immunity and disease resistance (Aguirre-Guzmán et al., 2012; Hayatgheib et al., 2020; Hoseinifar et al., 2017; Tacchi et al., 2011; Torrecillas et al., 2014). In the future, further studies are needed on the functional mechanisms of individual additives and their interactions, especially their synergistic effects. Usage of many such additives is however under strict regulations that vary widely among countries, although there are levels of regulation exerted on their use through global efforts such as Codex Alimentarius (http://www.fao.org/fao-who-codexalimentarius/home/it/).

2.3 | Future (2020 and beyond)

Analysis of the changes in the FCR values for most mainstream species demonstrates that improvements have been plateauing for some time and only smaller gains are now being made, leading to a point of diminishing returns for many species (Figure 1) (Naylor et al., 2009; Tacon, 2020; Ytrestøyl et al., 2015). Any future work on defining requirements needs to focus more precisely on refining estimates with further consideration of nutrient interactions and the use of new and more stable delivery forms, which help reduce nutrient wastage and increase efficiency. In the coming decades, aquaculture sustainability will remain a major concern. Water quality remains vital for aquaculture production and inadequate nutrition and feeding practices are known to deteriorate water quality. Thus, designing more efficient feeds through better knowledge of nutrient requirements, their appropriate balance, and effective delivery forms will improve nutrient stability and absorption and minimize nutrient waste. Likewise, refining feeding management practices to avoid excess nutrient load in the water will limit (or reduce) the increased oxygen demand following eutrophication, which can compromise fish health, welfare, and growth.

There is a growing need to prescribe the required levels of essential nutrients in the diet more precisely based on age, genotype, nutritional history, environment, farming system, and immune status, and the fish quality to deliver a "precision nutrition" approach to farming targets. This will necessitate the use of various modeling (using big data), internet-of-things (IoT), and artificial intelligence (AI) approaches to support aquaculture production and feed specification management. Integration between traditional models with more mechanistic approaches will lead to better prescription of nutrient and energy requirements based on an increasing number of input parameters. Advances in such modeling systems are now already accommodating demands for amino acids and net energy demands for various species (Hua & Bureau, 2019; Glencross, 2021).

The improved definition of requirements for key nutrients (energy, amino acids, and fatty acids) on a digestible and net basis is still required for most species and especially those in the developing world. The future of aquaculture nutrition will increasingly be based on precision and smart farming that will require a clear definition of nutrient requirements on a digestible and a net basis. This is particularly important in the context of encouraging the utilization of locally sourced ingredients. The shift toward increasing use of alternative ingredients in recent years has made it even more important to formulate diets on a digestible nutrient basis, not only because of the presence of antinutritional factors that can interfere with nutrient utilization but also because of the variability in the bioavailability of the nutrients required to formulate balanced diets (Boyd et al., 2020).

Some of these new ingredients have complex matrices that limit digestion and/or absorption of nutrients (e.g., algae) (Valente et al., 2021), highlighting the relevance of formulating on a digestible basis as is already performed in many other species.

Tailoring fish diets to produce value-added products able to respond to consumer's expectation will also gain importance in the future. This will include nutrient fortification of fish via their diet for children, pregnant women, and elderly people, by enrichments in omega-3 (especially EPA and DHA), selenium, vitamin D, and iodine. The capacity of farmed fish to not only increasingly supply protein for the world, but to also do so in a way that enhances the nutrition of the young and at risk will become increasingly important (Tacon & Metian, 2013; Thilsted, 2012). This food fortification/enhancement combined with a growing focus on food safety will enhance the role of nutrition as a critical control point in aquaculture.

Functional diets for challenging production periods and conditions will gain increasing prominence. Climate change and growing levels of intensification and the use of recirculating aquaculture systems (RAS) will increase the susceptibility of fish to alterations in environmental conditions that will increase stress, which will need to be mitigated. Functional diets that contain ingredients or additives that affect animal robustness and health will become increasingly important. Because production system environmental changes are expected with the growing intensification of aquaculture, it will be necessary to further investigate what positive effects functional diets will have, by identifying the most adequate ingredients and/or additives that result in improved animal performance and health. The formulation of diets for challenging times in the fish production process will be increasingly required. The use of various feed additives to help or mitigate the effects of stress through the year or seasonally will become increasingly common. Although the potential for formulating marine ingredient-free diets already exists for a vast majority of species, it is usually not cost-effective in most cases for carnivorous species. Such diets are also often associated with chronic health issues and poor animal robustness, so formulating based on nutrients (amino acids and fatty acids) will further require the search for additives that can be used to improve the general health status and robustness of different aquaculture species in a future with constraints on marine ingredient use.

Over the past 40 years, the rapid development and increasing intensification of aquaculture across a broad range of species and geographies have led to problems arising in some cases. Issues such as environmental deterioration and stress, sometimes leading to disease outbreaks and then subsequent abuses of antimicrobials and other chemical drugs, have been reported in various sectors. These issues threaten the food safety and sustainability of aquaculture. Misuse of antimicrobials not only leads to drug residues, affecting food safety, but also potentially leads to drug-resistant pathogens, which can then lead to public health issues. Many countries have legislated to prohibit the use of antimicrobials as growth promotors in animal feed (since 2006 in European Union), and many are gradually restricting its use for medical purposes to tackle the emergence of bacteria and other microbes resistant to antimicrobials. In addition, because of the constraints on further growth in the production of fish meal, fish oil, and other marine-derived ingredients, many nontraditional ingredients have been used to replace fish meal and fish oil in aquafeeds.

In many cases, this has resulted in growth retardation and impaired health of fish and shrimp as the changes were often not supported by science or backed up with required alternatives to bring a positive outcome. Hence, in the future, we must look for new technologies or nutritional approaches (e.g., functional feeds) to mitigate the negative aspects of substitutions of marine-derived ingredients and the reduction in the use and overall stewardship of antibiotics to ensure the good growth, health, product safety of aquaculture animals, and to enable the sustainable development of aquaculture. In parallel, there is also an opportunity to tailor flesh quality to increasing consumer's demand for healthier products. The fortification of aquafeeds with omega-3 (especially EPA and DHA), vitamin D, and minerals (e.g., selenium and iodine) can help provide adequate nutrition for vulnerable population groups (Kwasek et al., 2020; Thilsted et al., 2014).

Having defined the nutritional requirements of the various aquaculture species, there is additionally a need to find the appropriate raw materials (ingredients) from which to provide these nutrients and energy. This supply of raw materials also needs to develop sustainable supply chains to enable the aquaculture sector to continue to grow among the various sustainability challenges that the production of aquaculture feeds faces (MacLeod et al., 2020; Naylor et al., 2021).

3 | INGREDIENTS

There have been marked shifts in ingredient use for aquaculture feeds over the past several decades. In this section, we review the practices of the past and the present to predict future trends and needs. While not all aquaculture uses industrially produced compounded feeds, this is the fastest growing feed sector in the world and indicators suggest that more and more aquaculture production is becoming increasingly intensified and reliant on the provision of external feed inputs.

3.1 | Past (before 2010)

From the late 20th century to 2010, global aquafeed production grew from <5Mtonnes in 1990 to ~30Mtonnes in 2010 (Naylor et al., 2021; Tacon, 2020). Fish meal and fish oil were considered critical ingredients in feeds for many carnivorous fish and crustacean species, and their global production averaged ~6Mtonnes and 1MTonnes per annum respectively over this period. Fish meal use in aquaculture feeds peaked during 2005–2010 at ~3.6 Mtonnes per annum (Figure 2). Fish oil use peaked a bit before this at around 0.9Mtonnes per annum. Recognition that such marine ingredients were limited in supply led to a global effort to move toward more use of alternative ingredients in aquafeeds. Early fish meal alternatives were primarily of animal origin because of availability, cost, and protein content. Since then, the perceived risks associated with inclusion of rendered animal by-products in aquafeeds have seen their restriction in several geographic regions (primarily within European countries) because of concerns of pathogens and zoonotic disease transmission (Glencross, Baily, et al., 2020). Plant proteins were initially only a minor contributor to aquaculture feed protein and lipids for most carnivorous species, but by 2010, inclusion levels reached about 28% of the total feed inputs for salmon feeds globally, up from 12% in 2000. At the same time fish meal reduced from up to 45% in 2000 to 23% of the diet in 2010 (Ytrestøyl et al., 2015). This switch was initiated by several El Nino events, which reduced the availability of fish meal and forced the prices up. The feed production sector responded primarily by increasing the use of soy and some (wheat and corn) gluten meals. While much of the use of fish meal and fish oil prior to 2010 was driven by the economy of nutrients, plant proteins were seen to have significant limitations, often containing lower protein content, antinutritional factors, and imbalanced nutrient profiles (Gatlin III et al., 2007).

Although these constraints still existed for plant ingredients, reduced fish meal supplies and increased costs drove the demand for alternative protein sources. Terrestrial plant ingredients were generally considered as being

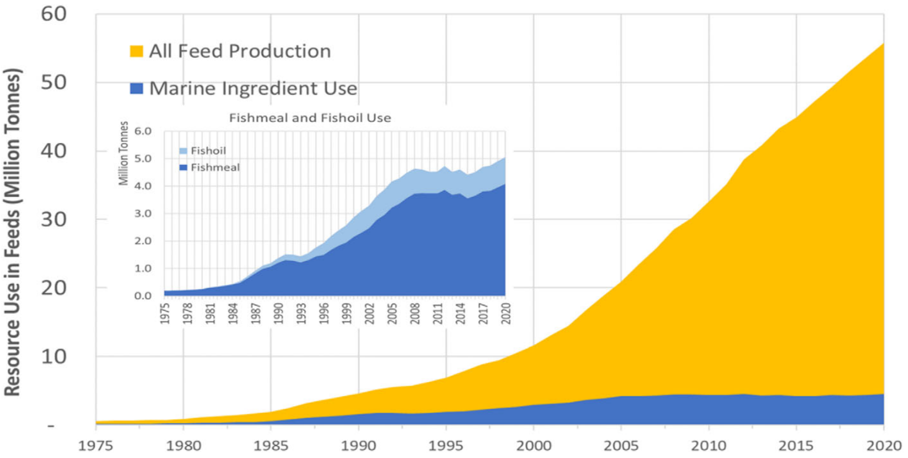

FIGURE 2 Estimated feed production for all fed aquaculture species sector from 1975 to 2020, with concurrent marine ingredient use across the aquaculture sector. Shown in the inset is a magnified set of the marine ingredient (fish meals + fish oils) use data across the same time. Data derived from FishStat 2020 and IFFO, 2021.

more sustainable and gained a more significant position in aquafeeds with new processing technologies leading to the creation of a variety of plant protein concentrates that could compete with the higher price and protein content of fish meal. Although still not widely used in feeds for carnivorous species, plant proteins and oils were already by this time the major contributor to aquaculture feed protein and lipids for omnivorous and herbivorous species. Soybean meal was already a widely used ingredient in feeds for omnivorous and herbivorous species, with other grains being used included a range of cereal, oilseed, pulse, and various grain legume seed products. Typical inclusion levels of soybean meal in feeds for such omnivorous and herbivorous species ranged from 15% to 45% (Tacon et al., 2011).

3.2 | Current status (2010–2020)

Presently there is ~55Mtonnes of aquafeed production globally, of which fish meal is now only ~4MT, fish oil is ~1MT, and the rest (~55MT) is mostly plant-derived resources (IFFO, 2021). Use of marine ingredients (proteins and oils) in aquafeeds has stabilized since 2010 and they are now seen more as strategic ingredients, with a growing use of by-product fish meal now contributing to >30% of all marine ingredient use in manufactured feeds (Hamilton et al., 2020; IFFO, 2021).

Plant proteins continue to be the main contributor to aquaculture feed protein and lipids for most aquaculture species, but their use is also seen as contentious in some circumstances (e.g., soybean use and associated deforestation concerns). Notably, feeds for carnivorous species are now predominantly composed of plant proteins and oils (Ytrestøyl et al., 2015). The increasing use of processing to produce protein concentrates from soy, peas, and other legumes as well as cereal glutens has occurred. This processing maximizes the protein concentration, quality, and suitability for use in feeds, while minimizing the non-nutritive factors (Drew et al., 2007). To balance the amino acids, the use of plant proteins and the concurrent reduction in fish meal has led to a much more complicated formulation, now involving a greater number of protein sources with addition of some crystalline essential amino acids to create a balanced diet to support high growth performance and healthy fish. This broader raw material array brings some advantages to the feed sector, in that it is not reliant on any one ingredient—so there is more resilience to supply chain threats (such as poor harvests). But plant proteins also bring some sustainability challenges to address (Malcorps et al., 2019).

The focus on soy and deforestation is probably foremost, which has led the feed industry to work with their soy suppliers in Brazil to set deforestation and conversion-free cut-off dates in 2020 for their entire supply chain. Plant proteins also typically have a much higher carbon footprint than fish meal, which has pushed the overall footprint of the feed up over the last 20 years (MacLeod et al., 2020). Carbon footprint is increasingly of interest, as the carbon impact of food systems has been publicly highlighted. Here aquaculture is in a very good position, being a typically low greenhouse gas (GHG) emitter compared with other animal protein production systems, but it also has a great opportunity to improve (MacLeod et al., 2020). It has been suggested that replacing 20%–30% of fish meal in shrimp feeds with plant protein ingredients could result in a 63% increased demand for freshwater, 81% increase in land requirements, and a need for 83% more phosphorus (Malcorps et al., 2019).

Across a broader range of life cycle assessment impact factors, it has been argued that there is insufficient land for the expansion of animal feed crop production (Popp et al., 2017), as it currently occupies roughly one third of global croplands (Robinson et al., 2011). Furthermore, there are additional pressures on land use because of population growth, climate change, and demands for food and biofuels (Godfray et al., 2010; Spiertz & Ewert, 2009). In their discussion, Malcorps et al. (2019) remind us that the Sustainable Development Goals of the United Nations include food security, hunger reduction, and protection of life on land and in the sea. They emphasize that minor price changes to crops resulting from increased pressure on land-based food production systems could have dire consequences in developing countries, where 50% of the household income is spent on food (Spiertz & Ewert, 2009).

The current focus is not only on the reduced reliance on fish meal and fish oil derived from capture fisheries but also increasingly on the overall sustainable supply of terrestrial and plant feed ingredients. Some of the raw materials used in aquaculture feeds can be consumed by humans, resulting in food-feed competition. There is also a consideration of whether raw materials that could be consumed directly by humans should be used for animal feeds.

The shift towards plant-based ingredients in aquaculture feed also faces competition from livestock and agriculture sectors, as well as biofuel production. Marine and terrestrial ingredient sources are both vulnerable to climate change, which may cause disruption and decrease in supply and higher costs for aquaculture feeds (FAO, 2018). There is thus a trend toward increased use of by-products as feedstuffs in aquaculture and livestock feeds with a growing focus on biocircularity of resources. However, consumer concerns have been raised in some markets around the use of by-products, in particular animal by-products that could bring a good nutritional input but are blocked from use in some supply chains because of perceived health risks and social objections (Glencross, Baily, et al., 2020). In parallel, circular proteins such as insects and microbial biomass are being increasingly advocated as sustainable alternatives, as they can convert various waste streams such as food waste, household waste, plant by-products, and sludge into high-quality nutrients. High production and processing costs still limit their large-scale production, and a range of regulations still limit their application in certain markets.

Both microalgal and genetically modified crops have been commercialized that produce long-chain omega-3 in industrial volumes (>1000 tonnes). Because of an urgent need for fish oil alternatives, a range of omega-3-rich ingredients are emerging, for example, microbial ingredients (microalgae), oil seeds with high level of LC-PUFAs (rapeseed and camelina), and increased use of fish by-products, and lower trophic marine species (e.g., krill, mesopelagic fish) (Hamilton et al., 2020). Up to eight relatively new sources of EPA and DHA with industrial potential for aquafeeds have been recently described (Tocher et al., 2019). These products included five microalgal sources, two genetically modified seed crop oils, and one yeast biomass. Identification of cost-effective, alternative lipids high in the LC-PUFAs EPA and DHA remains a substantial hurdle for the future of aquaculture. Both microalgal and genetically modified crops will undoubtedly play an increasingly important role in aquafeeds for those species requiring LC-PUFAs. Perhaps equally important is the need to fortify fish feeds toward the improvement of human health.

Food safety is a considerably overlooked aspect of much of fish nutrition research, but it is increasingly highlighted socially and politically (Glencross, Baily, et al., 2020). As an example, perceptions over the use of food waste for livestock and fish feeding have limited efforts in this area, particularly in developed countries, and yet there is an estimated 1.3 billion tons of human food lost and wasted each year (Gustavsson et al., 2011). Concerns over genetically modified feed ingredients also limit options in certain parts of the world, but others are readily adopting this technology. Food safety risks are associated with the possible chemical contaminants and biologically hazardous materials present in ingredients and feeds, which might be passed to humans who consume aquaculture products. Concerns have been raised about antimicrobial residues, persistent organic pollutants, heavy metals, mycotoxins, and industrial contaminants (Tacon & Metian, 2008; Glencross, Baily, et al., 2020). Additional concerns over microplastics in fish meal have been raised recently (Gündoğdu et al., 2021; Hanachi et al., 2019; Thiele et al., 2021).

3.3 | Future (after 2020)

It has been suggested that by the year 2050 aquaculture production is going to double and intensify (FAO, 2020). Fundamentally what will be needed to feed that production is sustainably sourced, economic, good quality protein, some essential amino acid (EAA) additives, some omega-3 options, various mineral and vitamin additives, and cost-effective energy sources. To achieve this will mean we need another 50MT of resources that we currently do not have or that are presently being used in other sectors. Although gains in crop productivity have kept pace with demand through most of the 20th century, they are not keeping up with demands more recently (Grassini et al., 2013; Schauberger et al., 2018). Notably, most currently used plant protein resources are also used in pig and poultry feeds (so a competition issue exists).

There is additionally the concern that many of these plant protein resources can be used directly to feed humans rather than animals. Add into the equation that there is a declining availability of freshwater, phosphates, and arable land, and it is obvious that terrestrial crop products are not the only solution going forward. Further competition for ingredients of plant origin is also occurring for human food and nonfood products such as biofuels. While many plant-source ingredients are considered economically sustainable, questions have been raised about their social and environmental sustainability, notably products from soy and palm oil production (Hospes, 2014; Okereke & Stacewicz, 2018). These constraints provide a strong argument for the development of nontraditional protein and oil sources.

Fish meal and fish oil are still considered among the most nutritious ingredients as they are rich sources of essential nutrients and have a high level of palatability in virtually all aquaculture species. Increasingly fish meal and oil production will come from by-product resources from fish caught for direct human consumption (e.g., Alaskan pollock) or aquaculture by-product. By 2030, more than one third of all fish meal and oil will come from by-product sources (IFFO, 2021). The continued reduction in the reliance on fish meal and fish oil, combined with the concurrent increased use of alternative raw materials in aquaculture feeds, highlights the need for an approach based on complementarity of ingredients (Turchini et al., 2019). The increasing use of alternatives brings about the need for a range of feed additives to supplement specific essential nutrients including essential amino acids, essential fatty acids, and trace elements. We may also see greater usage of bioactive compounds, prebiotics, probiotics, and other immunostimulants (Boyd et al., 2020). It is critical to find additional, cost-effective ingredient sources to meet the growing nutrient demand. This burgeoning demand, growing ingredient competition, and heightened sustainability awareness provide a strong argument for the development of nontraditional protein and oil sources, especially those part of the circular bioeconomy like insects, microalgae, microbial biomass, and food waste.

Technologies that produce protein, amino acids, and omega-3 using noncompetitive processes based on non-food grade resources (e.g., bacteria, yeasts, and algae; single-cell ingredients [SCI]) perhaps offer the most potential to generate the additional resources needed (Glencross, Huyben, & Schrama, 2020). As biotechnology advances, a broader range of substrates from various waste streams will be used in the fermentation process to reduce costs and increase profitability of SCI production. This will include the downstream processing to enhance the nutritional value of the microbial ingredients. As the competition for natural resources increases and technology advances, production of microbial ingredients will shift from being dependent on photosynthesis and products from this process as substrates toward use of cheaper input factors (e.g., organic acids, CH_4, H_2, and CO_2 gas) from industrial waste or other renewable sources.

Additionally, there will be increasing pressure to source ingredients locally for feed production and reduce dependence upon imported sources. This will demand more effort be given to use of local ingredients, the adoption of nutrient recycling, and use of innovative raw material processing techniques. This will probably be coupled with the use of renewable energies as the type of fuel used for processing has a remarkable life cycle impact on such ingredients (Campos et al., 2020). In the future, there is likely to be more competition for natural resources; driven by factors such as population growth, development of the bioeconomy, and climate change. Aquaculture production will play an increasing role in meeting the global protein supply and the need for feed to sustain this production will clearly increase.

Sustainability of different feed ingredient sources, including possible climate change impacts, is becoming a growing issue. For the global aquaculture sector to grow sustainably, it must have a sustainable supply of nutrients to make the feeds. The key sustainability issues vary from ingredient to ingredient and the historical approach was to focus just on one feed ingredient at a time, such as fishmeal or soy. Sustainability of different feed ingredient combinations will become a key defining characteristic of their utility, with increasing use of independent certification systems to verify claims. Going forwards, we will see an increasing focus on the sustainability of the feed ingredient supply chains. The discussion should move beyond whether an individual ingredient is sustainable or not, to one of whether that supply chain is. For example, fishmeal can be supplied sustainably, from sustainably managed fisheries. Soy can be farmed sustainably, on land that was not recently converted from native vegetation. Independent certification schemes have been established to provide verification of claims. There are a broad range of schemes with different levels of value and credibility, but all add cost to the overall supply chain. However, the expectation is that the use of certification to verify sustainability claims will continue to grow. As the topics covered by sustainability increase, the number of schemes is likely to continue to grow, for example, through moving beyond fisheries and deforestation issues to addressing issues of human rights, carbon footprint, land, and water use. The level of complexity to be managed will increase, but the information to do this has to keep pace, so good decisions are made on the latest reliable data. This can only be supported by a full value chain commitment to change, led from the consumer and retail end to support the upstream supply side's transformation. Without commitment from the market, changes will be harder to implement and value. Assessment of the sustainability of feed ingredients varies depending on the type of ingredients as their social, economic, and environmental impacts all differ considerably. There is a need for harmonization of various aquaculture-related sustainability certification standards to ensure consistency (Kok et al., 2020). The adoption of certification schemes will continue to reduce or eliminate ingredients from unsustainable sources.

Food safety will also become an increasingly important issue in the future. Driven by consumer perception, politics, and some level of science, consumers will gravitate toward those products that align with their attitudes, preferences, and expectations. Food safety will continue to be important for feed manufacturers and fish producers to meet consumer demand for disclosure of credence attributes. In addition to safety, these include origin, sustainability, and nutritional content. As such, both mandatory and voluntary labeling will continue to be strong drivers of the seafood market.

4 | FEED MANAGEMENT AND MANUFACTURING

4.1 | Past (before 2010)

Feed rationing systems and management of how much and when feed was delivered to the animal were largely based on prior experience or demand-based, relying on the animal providing feedback to the person feeding them. Most feeding was manual, using hand, blower, or other simple delivery systems. As such, feeding was a labor-intensive process (Ibrahim & Sultana, 2006). Traditional feeding regimes were based on the experience of the operators, considering factors such as weather, watercolor, season, and animal behavior among other things. The diet was selected based on price and/or feed manufacturer recommendations. The focus was on fish growth. Traditional end points for manual feeding were judged by farmers making decisions based on their experience and skills. This primarily entailed deciding what feed, when, and how much was delivered to the animal (Jobling et al., 1995; Paspatis & Boujard, 1996). Assessments of animal behaviors and interactions with feeds and the feeding process were somewhat subjective, although for certain species some simple tools, like feed trays, were used to assist the process (Tacon, 2002). For technologically advanced sectors, sensor-based feeding systems were emerging (Kadri et al., 1998).

Historically, many feeds were based on the use of trash fish and/or made on farm by the farmers. These may have initially been fed as intact trash fish or made into a moist mash with the use of other materials and binders or made into dried pellets using simple pelleting manufacturing systems (Hasan & New, 2013). With the growth and increasing technical demands on the sector, specialist feed compounders emerged and brought advancements in the various processes used in feed manufacturing. Additionally, the feed manufacturing sector played an important role in helping farmers, not only in the provision of feed inputs but more importantly in the management of the feed on the farm and in the use of appropriate environmentally sound husbandry practices. In many countries, the feed manufacturers were the closest contact in the value chain between the farmer and the government legislature (Tacon et al., 1995). Notable among the manufacturing introductions during this period was that of expansion extrusion, which was introduced into some sectors from 1980s onwards and by the 2000s became widely used across the developed world for most fish species, and increasingly was being applied in the developing world. Extrusion brought with it a range of technical advantages, including the ability to control buoyancy of feeds, dramatically increase feed fat levels, improve water stability, and reduce wastage because of dust (Barrows et al., 2007; Obaldo et al., 2000).

4.2 | Present (2010–2020)

In the present day, feed management systems in technologically advanced sectors are becoming increasingly computerized in modern developed-world aquaculture. Automated centralized pneumatic feeding systems using in-cage cameras, acoustics, and computer-based decision-making tools are widespread, resulting in a reduced level of labor (Aas et al., 2011; Reis et al., 2020; Waagbø et al., 2013). However, in the developing world where the majority of aquaculture still occurs, feeding is still largely a manually controlled and managed process with important labor demands and continues to be a significant rural employer (El-Sayed, 2013; Hung & Quy, 2013; Ng & Romano, 2013). Feeding end points are still largely judged by farmer decisions in combination with computerized algorithms. The interpretation of the fish responses is experience-based and depends on the experience and skills of the individual farmer.

The use of growth and energetics models is increasingly being applied for the evaluation and management of feeding regimes for various species (Cho & Bureau, 1998; Glencross & Bermudes, 2012; Liu et al., 2018; Zhou et al., 2005). The application of modeling helps reduce both the feed cost and the waste being discharged (Bueno et al., 2017). Historically, modeling focused only on evaluating the feeding rate, but increasingly, diet formulation, environmental factors, feeding frequency, feeding rhythm, and even animal behavior are all being taken into consideration.

Manufacturing of feeds in the developed world is now mostly based on modern extrusion technologies (Barrows et al., 2007). There has been considerable development of engineering technological capabilities in this area, allowing considerable control over the forming, cooking, and densification attributes of the feeds. Such engineering systems are highly complex but offer a substantial level of control over the pellet-forming process, enabling the user to have significant control over pellet density, durability, and oil infusion capacities (Sørensen, 2012). Shrimp feeds, despite still being predominantly pelleted, are beginning to emerge as extruded products through some companies (Obaldo et al., 2000; Soares et al., 2021). In the developing world, there is still widespread use of pelleting, mash, and trash fish feeding. Feed manufacturing in these regions, particularly in small-scale aquaculture operations, has continued to rely on an on-farm mash feed manufacturing approach, although extrusion is increasingly being used by many commercial feed suppliers in these parts of the world (Edwards et al., 2004; Merican, 2021; Tacon & Metian, 2009; Xu et al., 2007).

4.3 | Future (after 2020)

To increase sustainability of fish production and optimize fish product quality and animal welfare, it is becoming even more important to monitor and control the animal production process (Antonucci & Costa, 2020). By reducing the feed conversion ratio, farmers will have less waste and loss of nutrients to the water they farm in, and they will tend to reduce their overall carbon footprint. To achieve this, we need a better understanding of feed intake and its physiological points of regulation and how this is affected by production system (e.g., RAS, pond, or cage) and a range of other abiotic factors. In the future, we will see increasing use of mechanized and automated feeding in the developing world, matching that already being undertaken in much of the developed world. This use of mechanized and automated feeding will aid in improving production efficiencies (through less wastage) and animal growth rates (through higher intakes), and commercial quality (achieving the market requirement) by allowing for the better alignment of feeding with the demand and needs of the animals being farmed, but this will correspondingly reduce labor demands and employment in the sector. Already there are signs of increasing use of autonomous feeding systems in the developing world, occurring through the development of a variety of low-cost automatic feeding systems (e.g., https://www.efishery.com/).

The use of AI in feeding systems is emerging. AI is going to impact businesses of all shapes and sizes across all industries (Marr, 2020). The increasing use of centralized computer-controlled feeding systems and in-cage/in-pond sensors and cameras will increasingly make an internet-of-things system of control more feasible for feeding aquaculture species (Måløy et al., 2019; Martos-Sitcha et al., 2019; Mustapha et al., 2021). The development of complex algorithms and AI that monitors feeding behavior will be used to help make decisions about feeding management (Jones et al., 2012; Zhou et al., 2018). Coupled with more precisely defined energy and nutrient demands over various size classes, environments, genotypes, and in situ bio-loggers, the inclusion of a precision nutrition approach will complement completely automated feeding (Hvas et al., 2020; Zhang et al., 2020).

The use of automation and AI will lead to precision and smart farming increasingly becoming a focus. The use of big data applications may play a major role in improving the efficiency of the entire supply chain, with focus on food security, safety, and sustainability (Gilpin, 2015). These will provide an increased focus on the application of principles of precision fish farming (PFF) to shift feeding management from comprising largely experience-driven processes to become a more knowledge-driven procedure (Føre et al., 2018). PFF feeding regimes based on animal demands and farm targets, including specialized diet formulations, considerations of environmental factors, animal health, and/or quality and/or water quality will be included in the AI system to provide precise decisions for management of computer-controlled systems. Biological and system informatics will become combined to increase the precision control of fish farming. The use of intelligent sensors and monitoring will support the application of predictive models and simulation systems, leading to improved decision management and integration of operations that will enhance the overall precision control of fish farming operation (Føre et al., 2018). The use of models to predict environmental fluctuations and adjust feed distribution accordingly and autonomously to minimize feed waste and improve efficiency should be the primary goal for improved production efficiency in aquaculture. The optimal solution should be the use of real-time techniques that can determine the actual feeding behavior based on the appetite status of farmed fish (Adegboye et al., 2020).

There will continue to be increasing use of extrusion feed production, with increasing uptake in the developing world and development of novel extrusion applications for nontraditional species based on improved feed technical qualities and flexibility of the manufacturing systems used. This increasing shift to manufactured feeds across the developing world will result in an overall improvement in feed quality and resource utilization by the sector, further aiding a move away from the use of trash fish and farm-made feeds. However, further support to promote this in developing regions of the world is required. Additionally, because of the increased use of automatic feeders, there will be increased demand for the use of high physical quality nonclogging extruded feeds in these feeding systems. The increasing demand for functional feeds with specialist additives will see the emergence of nanotechnology to precision deliver certain high-valued compounds to the fish, by preventing them to be digested or metabolized at certain stages of the absorption process, allowing for targeted nutrient and nutraceutical delivery. Such novel encapsulation methods will enable the protection of certain labile functional ingredients from the damaging forces involved in extrusion.

5 | CONCLUSION

Many of the advances in nutritional understanding of aquaculture species over the past 20 years have come from an intense focus on a few species. However, it should be clearly acknowledged that part of the challenge of aquaculture nutrition is the diversity of species involved and that their requirements can be just as diverse. There is an urgent need to bring our understanding of many of the nonfocus species into the same level of understanding. Even with the well-researched species, there is a growing need to adopt a "precision nutrition" approach to the supply of essential nutrients and various additives in the diet based on age, genotype, environment, and immune status. Additionally, although marine-derived ingredients are still widely used in feeds, even salmon farming has now become a net producer of seafood. The widespread use of plant proteins and oils has underpinned the growth of aquaculture over the past 20 years, although there is a need to further diversify this resource base. The capacity for aquaculture to achieve this has been the result of decades of nutrition research (Naylor et al., 2021). The future will require further work in developing the potential of a range of additional sustainable feed protein and oil options, particularly those from the circular bioeconomy. Progress in feed manufacturing remains important, even though it has evolved from a simplistic exercise to a highly complex science with state-of-the-art engineering. Further application of advanced feed manufacturing is needed, as there is still widespread use of pelleting, mash, and trash fish feeding in the developing world. As ever, feed management remains critical to ensure the best use of the feeds produced. While aspects of this may have dichotomized between the developed and developing world, with a high reliance on manual skilled labor in the developing world, the use of advanced automated computer-controlled feeding systems in the developed world is a growing reality.

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DISCLAIMER

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