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A SWOT Analysis of the Use of Marine, Grain, Terrestrial-Animal and Novel Protein Ingredients in Aquaculture Feeds

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ABSTRACT
A variety of new feed ingredients are emerging in the aquaculture feed sector. While the technology readiness of these options varies across and within the new ingredient classes, it remains important to consider them in terms of the overall feed ingredient spectrum. In this review, the use of marine, grain, terrestrial animal by-product and a range of novel (e.g., bacterial and yeast) resources being considered as potential protein feedstuffs for use in aquafeeds is explored. In comparing the nutritional attributes of each of the ingredient classes, an assessment framework is applied based on understanding the critical knowledge required to be able to accommodate any ingredient in a formulation process. To further examine each of the different ingredient classes a Strength-Weakness-Opportunity-and-Threats (SWOT) analysis is applied, to enable some consideration of what future potential may exist across the spectrum and what risks and opportunities they may bring. It is noted that all ingredients have strengths and weaknesses, and that there is no such thing as the perfect ingredient. By better appreciating the positives and negatives of each ingredient, it becomes possible to increase adaptability in responding to the various opportunities for their use in feeds.

KEYWORDS
Fishmeal; grain; poultry meal; insect meal; single cell; by-product; processed-animal-protein (PAP); yeast

Introduction

Over the past 20 years there has been unprecedented growth in the aquaculture sector and predictions are for this to continue (Food and Agricultural Organization 2022). In 2020 global production of aquaculture was reported at around 63 million tonnes per annum. To sustain this production, about 46 million tonnes of feed were used (Figure 1). Based on projections by the United Nations Food and Agriculture Organization's (FAO) global aquaculture production is predicted to more than double and reach yields of 140 M tonnes by 2050. The FAO also predicts that much of this growth will shift from Asia to Africa over this period (FAO 2022). This also means that feed production needs to at least double to over 100 million tonnes during this time. One of the fundamental questions underpinning that projection is how to obtain the feed ingredients to sustain that growth and just as importantly, how can the sustainability of that growth can be ensured (Pelletier et al. 2018; Malcorps et al. 2019). In this review a range of novel resources being considered as potential sources of protein to underpin the future expansion of world aquaculture is examined. In doing so it enables a comparison of these novel protein ingredients against some of the existing ones to provide some context. Each of the various ingredients is further examined through a Strength-Weakness-Opportunity-and-Threats (SWOT) analysis to enable some consideration of their future potential and what risks and opportunities they may bring (Glencross et al. 2020a).

Characterization: Defining what we are considering

In considering the use of any ingredient for producing a feed for an aquaculture species it makes sense to

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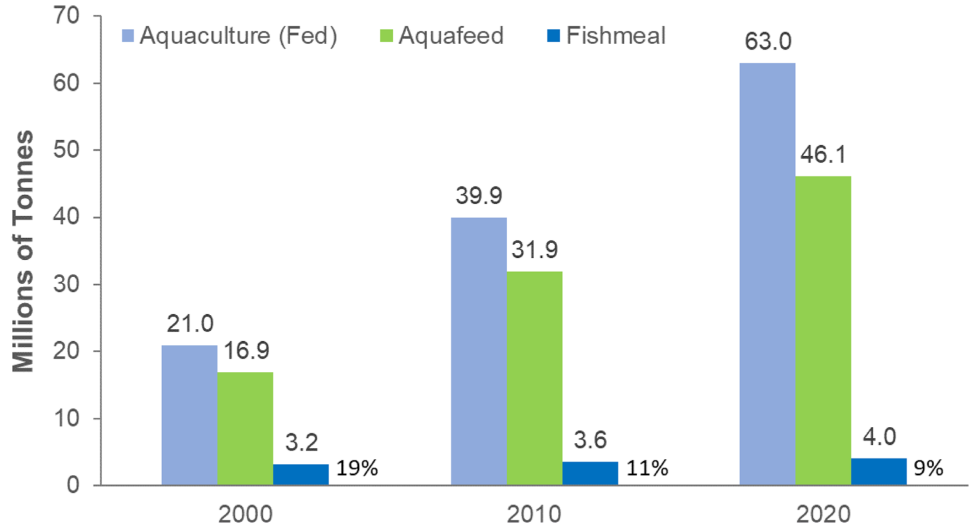

Figure 1. Global aquaculture production (fed species), aquaculture feed production and fishmeal use in aquaculture feeds (as absolute and proportional use) from year 2000 to 2020. All values millions of tonnes. Percent values are the overall inclusion of fishmeal as a proportion of total feed use. Data from IFFO 2023 and FAO FishStatJ 2022.

begin at the foundation. Understanding what it is that you are working with is arguably that foundation from which all further assessment stems. That assessment of the "what" is the characterization process, and this can involve the review of many different information sets (reviewed by Glencross 2020). Fundamentally, the feed industry usually demands this information from ingredient suppliers in the form of a technical data sheet (TDS), an information dossier that provides a range of characterization data so that a desk top assessment of the suitability can be carried out. Another valuable resource in this regard is the International Aquaculture Feed Formulation Database (IAFFD) which can be accessed at: www.iaffd.com. Other useful online resources and ingredient databases include that of Feedipedia: www.feedipedia.org/ and the United Nations Food and Agriculture Organization (FAO): www.fao.org/fishery/affris/feed-resources-database/en/. Additionally, for the terms of this review, it is important to characterize the various ingredients being examined so it can be clear about what is being described and what any subsequent evaluation refers to.

Marine ingredients are referred to those ingredients produced for feeds from either forage (reduction) fishery resources and by-products from both fishery and aquaculture resources produced for direct human consumption (DHC). This includes resources from fish, crustaceans, molluscs, and some other invertebrates (Shepherd and Jackson 2013).

Processed animal proteins (PAPs) include those resources made from terrestrial animals produced (usually) for DHC from which by-products are generated. Principally this includes poultry, porcine, ovine, and bovine meals. Typical products in this class would include meat-and-bone meals, meat meals, poultry offal (by-product) meals, feather meals, and blood meals. In a European context, this only extends to non-ruminant PAPs. In some cases, other PAPs are produced intentionally as a feed resource, included in this this class are also the insect and annelid meals like the other terrestrial animals, insects too are cultivated and come under similar biosecurity legislation as a feed ingredient (Ji et al. 2012; Li et al. 2017; Lock et al. 2018; Gasco et al. 2020; Carvalho et al. 2022).

A large variety of grain (cereals, oilseeds, pulses) protein sources exist, which are already widely used. In fact, plant proteins constitute the largest resource currently used in global aquafeed production. Principal varieties among those plant resources used either unmodified, or with varying degrees of processing include; Soybean, Pea, Faba (Horse) bean, Guar bean, Lupin, Wheat, Corn, Rapeseed, Sunflower, among others (reviewed by Gatlin et al. 2007). An additional application development being applied to plant protein resources in recent years is fermentation to improve their nutritional value, and this provides an additional aspect to the way we have considered using plant derived ingredients (Hamidoghli et al. 2020; Davies et al. 2021; Hossain et al. 2022).

The fourth class of ingredients examined are the single-cell protein resources (reviewed by Glencross et al. 2020b). These include ingredients produced from bacterial, yeast, fungal, or microalgal origins. Most of these ingredients are produced by using various fermentation or other culture systems of different designs.

Composition

When considering the nutrient composition of an ingredient, the first step is to consider the criteria on which we are formulating a compounded diet (National Research Council (NRC) 2011). Dietary nutrients are generally divided into four broad categories: protein (source of amino acids); lipids (source of essential fatty acids); vitamins and minerals. Energy, which is not a nutrient but rather in the biological context is the capacity to do work (metabolism), is obtained from the breakdown of lipids, proteins, and carbohydrates. Without this base level of information, it is not possible to formulate any feed with confidence as there will be holes in the formulation database. As a minimum a comprehensive analysis of the proximate composition (moisture, lipid, protein, and ash) of each feedstuff needs to be undertaken (National Research Council (NRC) 2011). From this assessment, the carbohydrate and energy content can also be estimated. Modern diets, however, are usually formulated to consider a range of other compositional parameters, such as contents of amino acids, fatty acids, minerals, and vitamins. So, the greater the characterization, the greater the utility of the information.

For most typical proteinaceous marine ingredients of animal origin, like both the North Atlantic and South American fishmeals, there is generally a consistently high level of protein (~65%) and moderate levels of lipids (~10%) (Table 1a). More broadly across the marine ingredient class, such protein meals are typified by their high protein levels (>50%) and moderate levels of ash (10% – 20%) and lipids (5% – 18%).

Notably, proteinaceous marine ingredients are essentially devoid of any carbohydrate content. The protein has a nutritionally favorable balance of essential amino acids, with levels of lysine, methionine, and histidine being high relative to many other protein sources. The lipids vary in their fatty acid composition but are typified by an approximate one third split between saturates, monounsatrates and polyunsaturates. Of the polyunsaturates, there is an abundance of long-chain n-3 fatty acids, notably eicosapentaenoic acid (EPA, 20:5n-3) and docosahexaenoic acid (DHA, 22:6n-3). The moderate ash content contains significant amounts of both calcium and phosphorus, both of which have nutritional value in animal feeds (Shepherd and Jackson 2013; Glencross 2020).

Processed animal proteins (PAPs) vary considerably across the different varieties subject to the material of origin (Table 1a and 1b). Some PAPs, like blood meals contain very high levels of protein (>80%),

Table 1a. Comparative compositional characterization of strategic and traditional protein ingredients. All values are g/kg as received unless otherwise specified.

	SAFM	NAFM	WGluten	CGluten	SPC	PPC	POM	HFM
Dry matter	918	918	956	905	919	904	968	958
Protein	670	677	766	610	626	496	702	913
Lipid	109	116	74	115	14	38	115	35
CHO	0	0	153	263	299	318	39	1
Ash	139	132	7	12	61	52	112	9
Energy (kJ/g)	20.1	20.5	23.6	23.4	20.5	18.7	21.8	22.9
Sum Amino Acids	620	659	761	608	553	468	549	818
Alanine	41	43	19	51	25	21	40	41
Arginine	39	43	24	18	39	43	41	58
Aspartate	58	65	25	37	72	56	39	31
Cysteine	9	8	4	3	2	7	10	42
Glutamate	83	96	301	132	113	83	47	49
Glycine	43	45	25	16	25	21	69	90
Histidine	25	15	14	12	10	13	13	9
Isoleucine	30	29	21	21	20	21	24	38
Leucine	50	54	52	96	44	36	43	69
Lysine	53	56	12	10	35	35	35	21
Methionine	20	23	13	15	9	4	14	7
Phenylalanine	27	28	39	36	30	23	23	40
Proline	27	30	100	55	31	20	51	116
Serine	22	31	41	33	34	24	26	89
Threonine	25	30	20	20	23	18	26	39
Tyrosine	21	25	25	27	19	17	19	21
Valine	37	36	26	26	22	23	29	58
Data Source	Glencross 2020	Glencross 2020	Glencross et al. 2021	Glencross et al. 2021	Glencross et al. 2021	Øverland et al. 2009	Li and Wu 2020	Li and Wu 2020

SAFM = South American fishmeal; NAFM = North Atlantic fishmeal; WGluten = Wheat gluten; CGluten = Corn gluten; SPC = Soybean protein concentrate; PPC = Pea protein concentrate; POM = Poultry offal meal; HFM = Hydrolyzed feathermeal. CHO = carbohydrates.

Table 1b. Comparative compositional characterization of various novel protein ingredients. All values are g/kg as received unless otherwise specified.

	FSM	FCM	BSF	BSFD	MW	MWD	SCP1	SCP2	YM1	MAM
Dry matter	907	911	917	923	931	940	951	963	940	966
Protein	502	475	423	511	524	648	715	509	466	688
Lipid	12	147	185	188	274	112	103	8	10	2
CHO	296	246	238	168	95	140	78	405	401	203
Ash	97	43	72	55	38	40	65	41	63	72
Energy (kJ/g)	17.4	22.4	21.4	22.4	24.8	22.1	21.9	19.3	18.3	19.8
Sum Amino Acids	513	527	431	489	532	485	574	421	424	679
Alanine	24	33	30	31	33	34	46	38	23	58
Arginine	35	13	28	34	37	48	42	33	20	52
Aspartate	59	34	43	42	51	23	56	44	35	43
Cysteine	9	13	1	2	3	1	4	3	0	7
Glutamate	114	77	57	65	80	26	71	63	132	68
Glycine	24	26	26	35	41	15	36	25	12	42
Histidine	15	16	13	15	16	22	14	11	9	13
Isoleucine	22	23	24	23	26	33	30	17	19	41
Leucine	38	52	32	34	39	51	51	33	31	63
Lysine	31	17	24	34	28	37	38	25	33	42
Methionine	5	19	9	14	7	10	18	9	3	22
Phenylalanine	27	20	22	21	23	30	29	20	22	39
Proline	24	84	30	34	38	13	26	19	18	31
Serine	25	23	16	19	21	25	22	19	13	43
Threonine	20	18	18	20	23	25	27	20	16	41
Tyrosine	18	24	33	41	39	52	25	14	16	38
Valine	23	35	33	35	37	46	39	28	25	36
Data Source	Shiu et al. 2015	Hossain et al. 2022	Basto et al. 2020	Basto et al. 2020	Basto et al. 2020	Basto et al. 2020	Glencross et al. 2023	Hardy et al. 2018	Huyben et al. 2017	Li and Wu 2020

FSM = Fermented soybean meal; FCM = Fermented corn meal; BSF = Black soldier fly meal (full fat); BSFD = Black solider fly meal (defatted); MW = Mealworm meal (full fat); MWD = Mealworm meal (defatted); SCP1= Single cell protein (Methylococcus); SCP2= Single cell protein (Methylobacterium); YM1= Yeast meal (Saccharomyces); MAM = Microalgal meal (Spirulina). CHO = carbohydrates.

whereas others like some insect meals contain only moderate levels (~35%) of protein. More commonly, ingredients in this class have total protein levels in the 45% – 65% range. Lipid levels are highly variable and highly dependent on processing factors. Some insect meals have high lipid (fat) levels >30%, whereas blood proteins tend to have very low (<5%) total lipid content. Most terrestrial vertebrate meals (poultry, porcine, ovine, and bovine) tend to have lipid levels around 8% to 15% (Table 1a and 1b). Most PAPs are generally known for their variable levels of ash (10% – 30%), depending on whether bone materials are included. PAPs can also have a considerable carbohydrate content, with meat, and meat and bone meals from ruminants sometimes retaining significant carbohydrate content from the animal's gut contents. Within insect meals, the level of chitin (a type of carbohydrate) can be as high as 15% of the meal and the nitrogen content of this amino polysaccharide can lead to erroneous estimations of protein. For this reason, estimations of protein content of insect meals that rely on the sum of amino acids are more reliable. Among the PAPs, there is generally a nutritionally favorable balance of essential amino acids, with levels of lysine, methionine, and histidine being high. The lipids vary in their fatty acid composition but are typified by a higher abundance of saturates, and monounsatrates, with only low levels of polyunsaturates. Of the polyunsaturates, there is an abundance of short-chain n-6 fatty acids, notably linoleic acid (18:2n-6). The moderate ash content contains significant amounts of both calcium and phosphorus (Bureau et al. 2000; Williams et al. 2003; Campos et al. 2017; Lock et al. 2018; Gasco et al. 2020; Carvalho et al. 2022).

Grain protein feedstuffs have perhaps the broadest variability in composition of all the different ingredient classes being considered (Gatlin et al. 2007). As with most cases, this is subject to the material of origin, though a notable effect of processing is evident (Table 1a and 1b). Some grain protein meals, like wheat gluten contain very high levels of protein (>80%), whereas others like pea and bean meals contain only moderate levels (<30%) of protein. There is no "typical" protein level for ingredients in this class. Lipid levels are also highly variable. Some oilseed meals have high lipid levels (>20%) before they are defatted, though in some cases full fat varieties are used in animal feeds. Other grain protein feedstuffs can be very low (<5%) in their total lipid content, often as a function of processing of the original grain to separate out various fractions (protein-starch-oil). Most grain protein sources are generally known for their low levels of ash (<10%). Grain protein feedstuffs contrast with most animal origin protein meals by containing a considerable amount of carbohydrates. The types of carbohydrates vary among the ingredient class, with some carbohydrates (starch) presenting significant nutritional value to many species, whereas other carbohydrates (lignin and cellulose), presenting little to no nutritional value (Hemre et al. 2002; Glencross et al. 2012; Kaushik et al. 2022). A recent addition to the grain proteins group, fermented grain, has a notable reduction in some classes of carbohydrates (Dawood and Koshio 2020). In particular, levels of soluble fiber are reduced in those grains undergoing a fermentation treatment. Among the grain proteins, there is high degree of variability in the profile of essential amino acids. Cereal derived proteins (wheat, corn, etc) tend to have low levels of lysine, whereas oilseed or pulse derived proteins (soybean, pea, lupin, etc) tend to be low in methionine. The lipids vary considerably in their fatty acid composition among the different products. Many plant products have proportionally high levels of monounsaturates and polyunsaturates. Of the polyunsaturates, there is tendency toward the predominance of short-chain n-6 fatty acids, notably 18:2n-6, though some plant products have low levels of the short-chain n-3, linolenic acid (18:3n-3). The low ash content has some phosphorus, though this is often unavailable biologically due to being present in the form of phytate. As the storage form of phosphorus in plants, phytate is an anti-nutritional factor (ANF), due to its chelating properties. Phytate is one of various forms of ANF that are also found in plant proteins (Francis et al. 2001; Glencross et al. 2020a). Anti-nutritional factors vary in both the type and concentration in the different plant resources, though in many cases they can be removed through processing (Drew et al. 2007).

In single-cell proteins (SCPs) there can be a widely variable composition observed within and among the different groups (see review by Glencross et al. 2020b) (Table 1b). Microalgal ingredient protein levels can be up to ~60% (mean = 34%); however, this is dramatically affected by the level of processing of the ingredient. Protein levels in fungal (yeast) ingredients are comparatively consistent at 30% to 60% (mean = 45%). Protein levels in the bacterially derived SCP can be as high as 80%, though typically are somewhat lower (mean = 60%) (Table 1b). Another feature of SCP ingredients is that there is often a notable difference between the two different estimates of protein, with crude protein (N x 6.25) being consistently much higher than the sum of amino acids (sAA) (Table 1b). In certain microalgal ingredients, the sAA is only about 70% of the protein value determined based on crude protein, and the way in which the microalgae is processed can also affect this (Teuling et al. 2017). In the yeast SCPs, the sAA value is more typically about 90% of the crude protein estimate; whereas those SCP produced from bacteria have a sAA value around 80% of the crude protein estimate. This lower sAA yield from bacteria is due to the high nucleotide content of the bacterial SCP which means there is much more non-protein nitrogen in the ingredient (Glencross et al. 2020b, 2023). The amino acid composition of the various SCP is markedly influenced depending on the organism used. Most SCP have abundant levels of leucine, lysine, and glutamate, though can be somewhat low in histidine and cysteine. The amino acid composition of yeast SCP resources are particularly rich in glutamate, but low in other essential amino acids like methionine, cysteine, threonine, and arginine. Bacterial SCP resources are high in leucine, typically the most abundant amino acid, along with that of glutamate and aspartate. In contrast to the other SCP ingredients, methionine is relatively abundant in the bacterial and microalgal SCP (Øverland et al. 2010). Many of the SCP resources are quite low (<5%) in lipid, reflecting the focus of many of these resources on protein production (Øverland et al. 2010; Glencross et al. 2020b). There are reports of certain genetically modified yeast varieties with high EPA (>30%TFA) levels that also have lipid levels exceeding 20% (Hatlen et al. 2012). There are substantial differences in the fatty acid profiles and total lipid levels among the different microalgal ingredients, and the various production and processing methods have a large impact on the fatty acid composition of the ingredients (Yaakob et al. 2014; Teuling et al. 2017). Certain microalgal SCP varieties are notable in their high levels of long-chain n-3 fatty acids, such as 20:5n-3 and 22:6n-3. Ash contents of SCP vary depending on how the different products are cultured and processed and can range from 0% to 40% of the ingredient but are more typically around 10% to 15% (Glencross et al. 2020b). Single cell proteins are also noted for certain other nutrients, like peptidoglycans, carotenoids and nucleotides that can bring additional bioactive properties. Bacterial peptidoglycans (e.g., Sanictum™) have been shown to stimulate the immune system in fish (Casadei et al. 2013) and shrimp (Sellars et al. 2014). Certain microalgae, such as *Haematococcus pluvialis* (NaturRose™) have been developed as natural sources of the carotenoid astaxanthin (Shah et al. 2016), as have certain bacteria (*Paracoccus* *carotinifaciens*; Panaferd-AX™) and fungal sources (*Phaffia rhodozyma*; RedStar™) (Sanderson and Jolly 1994). Both bacterial and yeast SCP resources have reportedly had levels of nucleotides as high as almost 16% of their biomass, making them amongst the richest sources of these compounds (Li and Gatlin 2006; Øverland et al. 2010).

Technology readiness

The technology readiness level (TRL) is a metric used for assessing the maturity of a technology as it transitions from basic principles and the concept through to full commercial implantation. Typically, there are nine TRLs, which are defined using a technology readiness assessment (Mankins 2009). The TRL process becomes pertinent to the feed ingredient story by providing an understanding where the realities of a new or novel technology or product thereof might lie in terms of being able to deliver credible supply outcomes to the feed sector and when this might occur and what needs to be undertaken to progress developments along the TRL scale. Their primary purpose is to assist management of such technologies and to identify where their development needs lie or the realism associated with the state of development at a given point in time, or other potential risk factors associated with the technology. It has been applied in recent years in terms of development of technologies like those of insect meals and SCPs in fish feeds (Gasco et al. 2020; Glencross et al. 2020b). For most academic research, the TRL are constrained to TRL1 to TRL6. From that point onwards, the commercial sector usually takes ownership of the process to further develop the technology in a relevant and operational environment. Another simple way to examine this facet is to consider the scale of production.

Marine protein sources have been well established as an industry for well over 50 years, predating the rise of aquaculture. The sector has long been considered as a well-developed, mature industry. In 2020, production scale was around the five million metric tonnes, with about two thirds of that volume coming from reduction (forage) fisheries, and the remaining one third produced from by-products and trimmings from both aquaculture and food fisheries (Glencross and Bachis 2021). Various modernization initiatives have occurred over the past twenty years across most of the industry, with well-established computer-controlled processing systems now existing in most major producing regions. Most importantly, the sector follows stringent regulations overseeing the allocation of fishery quota systems based on targeting a maximum sustainable yield (MSY) approach to the main reduction fisheries. This introduction of quota systems across the main fisheries has seen some rationalization of the volume of production down from seven million tonnes in the mid-1990s to current levels of around five million tonnes, which have been sustained since the mid-2000s.

There is some dichotomy in the TRL of processed animal proteins. The processing of terrestrial animal by-products from avian, porcine, ovine, and bovine origins has been well established for over fifty years and the sector can be considered as a well-developed, mature industry. In 2015, the estimated global production was around 15 million metric tonnes (WRO 2023). In addition to the modernization of the processing, there are stringent regulations overseeing the use of resources as raw materials (e.g., constraints to the use of ovine and bovine material), with a categorization system (cat.1, 2, or 3) established in Europe governing the types of raw material based on species of origin and biosecurity status (European Commission (EC) 2013; Glencross et al. 2020a). Specific legislation was introduced in Europe to regulate the use of processed terrestrial animal by-products as feed ingredients as a means of restricting the incidence of transmissible spongiform encephalopathy outbreaks (European Commission (EC) 2001, 2013).

As regards proteins from insects, although the production of black soldier fly larvae as a feed ingredient has been considered for many years, it is only in the past decade that the scale of production for this purpose has become large enough to approach being economically viable (Lock et al. 2018). Numerous startups and commercial ventures have been initiated over the past decade, with considerable application of venture capital funding being applied to the development and upscaling of industrial scale insect production systems (Lock et al. 2018; Gasco et al. 2020). Like any new industrial sector, there have been various issues that have needed to be addressed for the viable upscaling. Chief among those issues has been the need to identify and obtain suitable feed substrate for the larvae (Lock et al. 2018). An important attraction of using insect production systems, as a means of producing value-added feed ingredients, was based around their capability to convert low-value agricultural waste streams into high value feed and/or food ingredients. In Europe, legislation has been introduced that constrains the use of non-food grade waste streams as feed resources for insect farming. This has meant that most animal waste streams cannot be utilized as substrates (EFSA 2015; Lotta 2019; Veldkamp et al. 2022).

Grain products represent the largest feed resource by volume globally. Soybean production alone in 2020 was estimated at over 350 million tonnes globally (Our World in Data 2023). Cereal products, like wheat, corn and rice are at production scales in the billions of tonnes per annum. While for some aquaculture species the use of unprocessed grain products has some commercial application, for others there is a distinct need to process plant products to produce protein concentrates and isolates (Gatlin et al. 2007). Large scale production of protein concentrates and isolates from soybean, rapeseed, wheat, and corn for instance has been commercially available for some time (Kaushik et al. 1995; Refstie et al. 2005). Fermented grains are a variant on the standard applications of grain products, which allow for the reduction of some specific antinutritional factors for instance in soybean. Despite some examples of commercial scale fermented plant products sources, it is notable that much of the research undertaken over the past 10 years still relies on noncommercial sources (i.e., laboratory made samples) (Mukherjee et al. 2016), suggesting that parts of the sector are still at a TRL of 3 to 7.Despite what has been published in academic journals though, there are reports of volumes of fermented protein products in the 100,000s of tonnes being produced in association with bioethanol production that are already being marketed toward aquaculture and pet foods (Green Plains 2024). Genetically modified (GM) plant products make up extensive amounts of the global production of soybean, corn, and rapeseed (Kumar et al. 2020). As such the TRL of GM grains is regarded clearly as level 9, (proven in an operational environment). As can be ascertained by the level of acceptance and use across the world, the TRL for GM technology is already well established under an operational environment and continuing growth and pressures are likely to continue to see further adoption by the aquaculture sector of such feed ingredients.

Single cell proteins are another novel ingredient that is approaching higher levels of the TRL, but there is considerable variability in where different products fit within that scale (Jones et al. 2020). Some bacterial SCPs are now entering levels 8 and 9 of the TRL with projects producing industrial scale amounts of protein recently announced and/or delivering product (Calysta 2022). There remain other projects which are still at TRL levels 5 to 6 or even lower, despite much publicity (Sharif et al. 2021). The microalgal protein product subset of the SCPs still requires some work to develop critical mass. While projects developing lipid sources from microalgae appear to have been successful in reaching critical mass, only Spirulina production has achieved notable volume of scale in terms of proteinaceous products (Jacob-Lopes et al. 2019), but mainly aiming at application in the food rather than feed sector. Various impediments to scale up for microalgal proteins have been noted, key among them being an effective means to disrupt and separate cell walls from the cell contents. Other major hurdles identified for this sector include the need to develop technologies or at least better adapt current technologies (heating, filtration, and centrifugation) that can collect, concentrate and dry materials in a cost-effective manner without affecting the nutritional quality of the product. Many of the principal barriers that need to be overcome for large-scale adoption of alga products for aquafeeds are the same as for yeast and bacterial products, namely, the costs associated with large-scale production, harvest, and processing (Glencross et al. 2020b; Jones et al. 2020).

Cost

Fundamentally, the business of aquaculture is undertaken for both food production and profit. Without some form of profit (either as food provision in subsistence systems or monetary in business-based systems), then the process will rapidly cease. Because of this, the costs of feed ingredients become an important consideration. The cost of an ingredient is not only influenced by the price of the commodity, but also the price that must be paid for shipping and storage prior to incorporation into a feed. The aquaculture feed industry is very competitive and most modern feed manufacturers use least-cost calculations to fine-tune formulations. Least-cost formulations allow a producer to swap out portions of ingredients in a feed formulation and replace it with some other ingredient based on cost or cost per unit of nutrient (e.g., $/%protein). Over the recent past, more than "least-cost" considerations, including issues such as least-risk (feed/food safety) and societal issues (sustainability, environmental footprints, labour) have become major drivers.

Regulatory constraints

Even if nutrient and practical considerations are accounted for, it may not be possible to use certain ingredients because of regulatory considerations. There are several reasons that regulations may prevent or limit the use of specific ingredients. Many of these involve environmental, health and/or safety concerns. Key food safety concerns include those related to the real or perceived threats of food safety concerns (Glencross et al. 2020a; Regueiro et al. 2022).

Regulation of toxic contaminants is undertaken by various parts of legislation and/or guidance documents with key entities in this regard being Codex Alimentarius (CODEX) and the European Food Safety Authority (EFSA). Both organizations have developed numerous recommendations on the setting of maximum residue levels (MRLs) for a wide range of contaminants, including certain heavy metals (e.g., As, Cd, Hg, and Pb) and a variety of persistent organic pollutants (POP's), including dioxin, polychlorinated biphenyls (PCBs), and poly- or per-fluoroalkyl substances (PFASs). EFSA also passes advice (opinions) to the European Commission (EC) for passing into legislation. Such legislation currently extends to not only the level of contaminants in feeds, but also their MRLs in certain feed ingredients. Such restrictions on the MRLs of various contaminants places some constraints on the potential of some materials as feed ingredients, as they may be natural accumulators of certain contaminants, such as with cadmium and soybean production or exposed to higher levels of environmental contaminants by their nature of production, such as with fish oil production from species in the Baltic sea (Cataldo et al. 1981; Nicholson et al. 1999; Berntssen et al. 2010; Wang et al. 2013; Tao et al. 2020).

In addition to the regulation of feed ingredients for zoonotic threats and chemical contaminants, there are also issues as regards the use of genetically modified organisms (GMOs) in feed and specific labeling requirements in this regard within the EU. These have been published for almost 20 years (European Commission (EC) 2003a; European Commission (EC) 2003b). Notably, the EFSA GMO panel recently released an updated scientific opinion for the re-authorization for the use of three GMO varieties of soybean in the EU (EFSA GMO Panel 2022). European legislative (1829/2003 and 1830/2003), and labeling requirements specify a threshold of >0.9% for the presence of recognized GMO products (European Commission (EC) 2003a; European Commission (EC) 2003b). It may be noted that the European regulatory system operates on a heightened risk aversion policy relative to many other regions around the world, largely as a response to persistent food-scares in that region in the late twentieth century (Glencross et al. 2020). Principles, such as the as-low-as-reasonably-achievable (ALARA) practice form a key doctrine of groups like EFSA with respect to food and feed contaminants, and as such the European regulatory system is often seen as the leader in terms of food and feed regulations, with many other regions following suit once EC regulations are established.

Societal constraints

A variety of societal constraints exist over the choices made for use of resources as animal feeds. It is obvious however, that not all food resources are suitable for direct human consumption. This might be for a variety of reasons including sanitation, logistics, or simple preference issues. When we consider raw material resource use in the form of a hierarchy, this option of feeding food to an animal is clearly a secondary choice, but in some instances, it remains the best option available (Stevens et al. 2018; Malcorps et al. 2021). While prevention of food waste, and optimization of distribution are considered higher priority options ahead of feeding resources to animals, the use of food resources as feed, remains the next best option to retain valuable nutrients within our food-chain. Beyond the use of such resources for feed, the subsequent options are all about waste management and nutrient recovery (Figure 2).

Marine ingredients have a crucial issue that dictates the way in which the resource that underpins it is managed from a societal perspective. Notably, the raw material is highly perishable and presents food sanitation issues if the cold chain is not managed appropriately. The marine ingredient sector further has significant logistics issues with a considerable amount (sometimes millions of tonnes) of its volume being produced in very localized regions and on a very seasonal basis for only a few months of the year. The production of anchoveta on the west coast of South America each year is one example of this, where it occurs from the north of Peru to the north of Chile and is largely confined to two distinct, three month seasons each year. This boom-and-bust nature is something quite typical of many low-trophic species found in high abundance on a seasonal basis and is also subject to natural phenomena such as El Niño events. From these two fishing seasons each year the Peruvian industry alone harvests around 4.5 million tonnes of fish to produce around a million tonnes of fishmeal and 200,000 tonnes of fish oil (Shepherd and Jackson 2013). Although various projects have been attempted to encourage direct consumption of anchoveta in Peru, the abundance of a wide range of other, more preferred species in the region mean that there is little to no viable market locally for the species (Avadi and Freon 2015). Both canning and freezing the product have been evaluated but continue to remain uneconomical. Consequently, the best

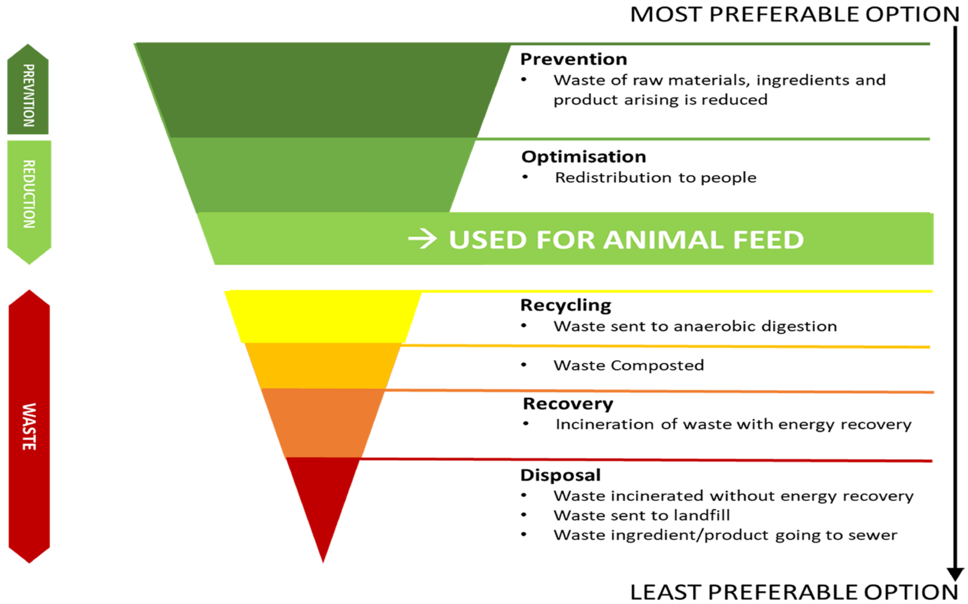

Figure 2. Conceptual optimization of food waste use hierarchy.

remaining option for use of the resource has been to dry and stabilize (inclusion of antioxidants) the product so that it can be used as a feed resource over the following six to 12 months (Fréon et al. 2014; Avadi and Freon 2015). It is worth noting that a significant volume of the anchoveta oil is making its way to direct human consumption (IFFO 2023).

Processed animal protein sources have had a long history of being part of the human food chain. This does not extend to all sources however, with little history of products like feathers or poultry offal being part of the human diet (El-Haroun et al. 2009; Campos et al. 2017). The recent renewed enthusiasm to produce insects for feed also complements the long-term use of such resources for use as food, and notably much activity remains directed to this end (Lock et al. 2018; Lotta 2019). As with the examples presented for marine proteins, the perennial question with PAPs remains as to whether to use them as food or feed. There are various factors that likely influence the outcomes to this question, among them being market preferences, sanitation, and biosecurity (Lotta 2019). More recently, larvae of the lesser mealworm (*Alphitobius diaperinuslarva*), has been approved as a novel food for humans by EFSA and the European Commission (EFSA 2022; EC 2023).

The societal implications on the use of plant proteins in aquaculture feeds have several layers of complexities (Malcorps et al. 2019). Undoubtedly, the more than 300 million tonnes of soybean that are produced globally each year, could easily be directed to human food consumption. Notably, one of the main co-products, the oil, is mainly used as human food. The global soybean industry has well established logistics and few sanitation constraints. The product is a highly nutritious grain, rich in valuable protein and oils. It is largely a matter of preference however, that most of the world prefers to eat animal products rather than soybean, and consequently the majority of soybean is diverted to produce those meat food resources instead (Jia et al. 2020). Likewise, for other plant protein resources, there are always potential food options for using these resources in the human food chain. Many of these issues though, are about food quality rather than bulk nutrient or energy supply. That almost half of global grain production is used in animal feeds arguably occurs because most people would rather have meat in their diet rather than resort to being vegetarian or vegan. Another societal issue revolves around the use of GM technology. While the use of GM grains in fish feeds has been accepted practice in the Americas (North and South), and Asia for some time, there is reluctance to use them in aquaculture feeds in Europe (Glencross et al. 2020a). This reluctance is driven largely based on perceptions of consumer resistance and active lobbying by environmental non-governmental organizations (eNGOs) to directly influence retailer practices (Faccio and Guiotto Nai Fovino 2019). The outcome of this has been the European industry practice of preferentially using non-GM soy protein concentrates sourced at a premium and the use of other European origin non-GM grains. Legally, there is no impediment to the use of GM-grains in the European Union (or UK and Scandinavia) and indeed they are widely used in terrestrial animal (pig and poultry) feed and direct human food consumption, so the reluctance to use them in aquaculture feeds exists as something of a conundrum (EFSA GMO Panel 2022). While certain sectors, like the European Atlantic salmon production might continue to refrain from GM protein sources, the remainder of the global aquaculture feed industry is likely to continue widespread use of such ingredients.

Single cell proteins remain a relatively unknown entity in terms of their societal perception for use in animal feeds (Carter and Codabaccus 2022). Although in one form or other they have been around for over 50 years, their lack of widespread use has meant that there has been little established perception on their use.

Environmental constraints

Environmental constraints associated with ingredient use are another parameter of increasing importance (Papatryphon et al. 2004; Boyd et al. 2020). There have been various metrics proposed and claims made as to what constitutes a valid assessment of the environmental footprint of an ingredient (De Vries and de Boer 2010; Cashion et al. 2016, 2017). Fundamentally though, this must be about the holistic sustainability of food production systems around the world. To assess this various metrics have been proposed to measure the environmental footprint of many products and processes. The method gaining most favor and utility over the past decade has been that of Life Cycle Assessment (LCA). The LCA approach to sustainability of food production systems aims to compare a large range of environmental effects assignable to defined products and processes by quantifying all the inputs and outputs associated with various material and energy flows and assessing how these flows affect the environment (Ott et al. 2023). To achieve such an assessment an inventory is compiled of all the relevant energy and material inputs and environmental releases associated with the defined product or process. This inventory is then used to undertake a characterization of emissions; whereby different emissions are standardized into equivalents.

An important element of the LCA story, is that it is not limited to just carbon footprint but can address up to 18 different environmental impacts (Silva et al. 2018). Importantly, how you undertake a LCA analysis can have notable impacts on the interpretation. Features like the reference unit of assessment chosen, the system boundaries assessed, and the method of partitioning impacts between co-products from the same process can all be influential (European Commission 2018). Because of these constraints, there have been various attempts to set some methodological standards; for example, the International Standardization Organization (ISO) initiated the ISO 14040 series, whereas the EU developed the Product Environmental Footprint Categorization Rules (PEFCR) approach. To act as a standard setter and as a centralized independent repository for the feed industry the Global Feed Lifecyle-Assessment Institute (GFLI) was established and has freely available databases and tools (GFLI 2023) to aid consistent assessment.

Energy consumption and consequences thereof of capture fisheries and aquaculture has been a subject of interest for more than twenty years (Tyedmers 2000, 2001). Production of marine ingredients from anchoveta contributes 15% of the global biomass of fish caught but has amongst the lowest carbon footprints of all fisheries with just 3% of the global fishery related carbon-emissions (Parker et al. 2018). Although the carbon-footprint of anchoveta derived fishmeal is remarkably low, and no pesticides or herbicides are used, it does have a significant reliance on biotic resource use, another LCA impact category sometimes applied to aquaculture (Papatryphon et al. 2004; Fréon et al. 2017). Presently some 4.5 million tonnes of fish are harvested from the Peruvian anchoveta fishery each year. Despite this enormous volume of harvest (the largest single species fishery in the world), the broader impacts on biodiversity have been reported to be comparatively small compared to most forms of agriculture or even other forms of fishing, like trawling (Avadi and Freon 2013). Assessments of the broader ecosystem trophic impacts have been suggested to be nominal (Free et al. 2021). Fishing industries the world over though, have been the subject of much questioning over their sustainability, especially due to the issues of unsustainable, undeclared, and overfished fisheries across the world (FAO 2022). Recent data from Hilborn et al. (2022) has demonstrated that small pelagic fisheries, such as those for anchoveta, are among the most sustainable of all global fisheries. It should be noted however, that significant restructuring of fishing effort in the late 1990s and early 2000s was required to ensure the maintenance of the biomass close to the optimal maximum sustainable yield (MSY) biomass, where it has now been maintained for almost 20 years. This introduction of modern effective fisheries management has necessitated not only a reduction in fishing effort, but also the introduction of independent stock assessment, quota setting arrangements, fishing zone restrictions and extensive fishing vessel monitoring to ensure the resource use is sustainably managed (Hilborn et al. 2022).

Various environmental constraints have been raised with the production of processed animal proteins for use in aquaculture feeds. While those PAPs that are produced from the by-products of food production for direct human consumption (DHC), could be argued to have few environmental impacts, the production of animals for food underpinning that production are well recognized as one of the largest sources agricultural related carbon-emissions, especially so from production of ruminants (Moumen et al. 2016). The allocation of environmental burdens based on an economic allocation, results in most of the environmental burden associated with animal production being directed toward its primarily application of meat for DHC. This means that the environmental burdens associated with the by-products are comparatively small (Campos et al. 2020). Production of insects, however, presents something as a contrast, as they are usually not produced for DHC but rather as a feed ingredient. This production of an insect PAP therefore attracts all the associated environmental burdens of the production process and resource usage involved. While the potential to utilize low value food and other agricultural waste streams is promoted as an important feature of insect production, this still consists of a trophic loss of energy and protein and remains an environmental weakness of insect PAP production (Wehry et al. 2022).

Environmental issues of biodiversity loss, carbon-emissions, resource (biological, energy, etc.) use exist with the production of any food and feed resources, but production of some varieties of grain protein resources provide excellent case studies in this regard. Global soybean production is dominated by five main producing countries (USA, Brazil, China, India, and Argentina), annually each producing more than 10 million tonnes (da Silva et al. 2021). This production often conflicts with ecological considerations as the growth of those grain industries increasingly conflict with natural resource management ideals (da Silva et al. 2021). There have been a range of negative ecological issues linked with such terrestrial agricultural systems. Among them include, widespread deforestation, which leads to broadscale biodiversity depletion and results in large amounts of carbon-release each year (Jia et al. 2020; da Silva et al. 2021). Crop production itself produces enormous amounts of soil loss and carbon emissions from the fuel used and incurs the widespread use of insecticides and herbicides, that further contributes to a host of other ecological threats (Jia et al. 2020). There are also other contentious issues such as deforestation and biodiversity loss. While the contentious issue of deforestation might mostly be limited to some low-middle-income-counties (LMIC) countries and even regions within them, it must be acknowledged that this issue is one of temporal dissonance, with all other regions of agricultural activity simply having done the same at some earlier time. Arguably no agricultural cropping system anywhere can be insulated from issues of land clearing and biodiversity loss.

Single cell proteins, depending on the type can provide some significant environmental advantages in that some of the bacterial strains directly consume CO_2 or CH_4 as part of their production (Jones et al. 2020). Studies examining the LCA assessment of such systems have indicated that in some instances that SCP produced using specific substates may not have clear environmental footprint advantages over many other ingredients (LaTurner et al. 2020). Other SCP types, like yeasts can make use of under-utilized agricultural waste streams as energy sources, though they still need a source of organic nitrogen, and this remains an environmental weakness of yeast production (Agboola et al. 2021). Microalgal SCP sources, like some of the bacterial types, can also use CO_2 in their production and for the most part (excepting some thraustochytrid species) are generally regarded as photoautotrophs. Reviews of the broader LCA impact of microalgal sources shows varied impact profiles largely linked to energy used in the drying stages (Smetana et al. 2017).

Nutritional value: How ingredients interact with animals

In defining the nutritional value of any ingredient for an aquaculture species there are a series of factors which need to be considered that influence the capacity of a feed formulator to use that ingredient. Once the characterization of an ingredient has been completed, the next information required is that of palatability and digestibility (Glencross et al. 2007). These two nutritional value assessments, critically, must precede the subsequent assessment of utilization to ensure that any growth studies using the ingredient can be undertaken in a meaningful way, by ensuring that differences in nutrient supply between diets are minimized and that palatability differences accounted for (Glencross 2020).

Palatability

Palatability refers to the factors that influence the commencement and continuance of a feeding response

(Glencross 2020). The palatability of a whole diet or feed is influenced by its ingredient composition, and this can be very species specific. No matter how nutritious an ingredient or feed is for an animal, if it is not palatable then it will not be effective, unless remedial measures can be undertaken to overcome this. Good quality fishmeal and fish oil are known to be very palatable for fish, but many alternative ingredients are less so. Plant originated ingredients are frequently of low palatability, and this can limit their inclusion level in feeds. It is possible that a strong feeding stimulant, an ingredient that imparts high palatability even at low inclusion levels, can overcome palatability issues, at least partially (Adron and Mackie 1978). Krill products are examples of feeding stimulants that have been used to improve acceptance of feeds that would otherwise be of low acceptance by fish because of inclusion of unpalatable ingredients (Smith et al. 2005).

The primary point of interaction of any animal with its feed is initial perception. Up to 85% of growth-related variability has been linked to this point of interaction when feeding balanced diets formulated to digestible nutrient equivalence, implying that other factors such as variability in digestibility, and nutrient supply issues can only explain 15% or less of the variability (Glencross 2020). This perception depends on a process of olfaction, gustation, and ingestion, and in that order. Though for some species vision and vibration also contribute significantly. The animal must first sense the presence of food, and usually this is through vision, vibration, or olfaction (smell), from which it then orientates to the food (or not) and makes a choice as to whether to accept it or not (gustation). Following these initial interactions, the animal then needs to decide as to whether it consumes to the food (or not) resulting in its ultimate ingestion (Glencross 2020). How well the animal accepts the food is often used as the basis to define palatability. Various experimental strategies have been devised to test for this in both fish and shrimp, but arguably nothing is more robust than simply feeding the animal a feed and measuring its level of acceptance and ingestion. A range of consideration need to be made in such an approach, including the diet design, the effective inclusion level of the ingredient being assessed, what other ingredients might be used alongside it (complementarity), and for how long the intake might be assessed for (Turchini et al. 2019). Notably, sensory factors appear to be at their most sensitive over a period of seconds, minutes, hours, and days. Beyond this into days, weeks, months and so on, other satietal response factors linked to energy balance appear to predominate (Yasuoka and Abe 2009; Volkoff 2019). As such, it makes most sense to undertake such palatability testing over a period of no longer then two -weeks, though omitting the first couple of days which seem to be largely a period of confusion for the animal as it adapts to the new sensory aspects of the feed (Glencross 2020).

Marine protein sources have long been regarded as among the best of all the different ingredient classes for enhancing the palatability of aquaculture feeds (Smith et al. 2005). In many cases, this is arguably one of their more valuable features. Various studies have examined the inclusion of different ingredients and measured the feed intake (palatability) responses by different species in response (reviewed in Glencross et al. 2007). In some cases, the replacement of fishmeal using this approach has allowed the estimation of thresholds for marine ingredient inclusion to ensure diet palatability, with estimates ranging from 10% to 20% for fishmeals, with even lower inclusion levels effective for marine ingredients like hydrolysates (Smith et al. 2005; Glencross et al. 2011, 2014). The variability in ranges highlights several things. Notably, that there are certain preferences by some species for certain types and/or combinations of marine ingredients. Even among marine ingredients distinct differences in palatability have been noted within some species (Glencross and Bachis 2021).

Processed mammalian and avian protein feedstuffs have generally reported good acceptance in the diets of most aquaculture species. Thresholds for blood and feathermeal products have been reported at around 10% due to a decline in performance related to feed intake, suggesting palatability of these products may be tolerated to a certain limit, and usually whilst there were still sufficient marine ingredients in the diet (Bureau et al. 2000). Other mammalian and avian PAPs have reported higher effective inclusion limits, suggesting that these ingredients have less palatability issues (Williams et al. 2003). Similarly, processed (and unprocessed and alive) insect protein sources have also been apparently well accepted by most species in which they are tested (Lock et al. 2018; Hua 2021). For the most part, inclusion levels of insect PAPs have been restricted to less than 20% of the diet. Above this inclusion level, a reduction in growth due to a decline in feed intake has been reported (Hua 2021). Recent studies have shown that it is possible to exceed 20% inclusion in diets of some species without impacting regulation of feed intake (Basto et al. 2021, 2022)

Grain protein resources are usually notable in that their palatability characteristics are at best neutral, though more often poorer than that of most other resources. Importantly though, fish palatability preferences can vary markedly amongst the various aquaculture species and can be quite species specific (Glencross 2020). Some omnivorous species are less influenced by the inclusion of grain protein resources; whereas carnivorous species and those relying dominantly on chemoreception rather than visual sensory systems, like shrimp, can be comparatively sensitive to the inclusion of certain grain proteins (Smith et al. 2005; Gatlin et al. 2007). The inclusion of fermented grains in feeds for various aquaculture species has resulted in reports of improved feed intake relative to the feed intake observed for non-fermented grains (Refstie et al. 2005; Sharawy et al. 2016). Although fermentation of grains appears to provide some improvements to grain product palatability, the overall benefit on feed intake appears somewhat nominal, as there are still clear constraints to the overall inclusion level of fermented grains. At higher inclusion levels, a clear decline in feed intake is still observed as inclusion levels increase (Refstie et al. 2005; Yamamoto et al. 2010). The use of GM grain protein products does not appear to have had any significant impact on feed intake responses by fish in the various feeding studies reported. No effect on feed intake of a GM variety of lupin was observed when compared against its parental variety (Glencross et al. 2003). Sanden et al. (2006) also observed no differences in feed intake by Atlantic salmon parr fed either GM soybean or GM corn products when compared against their non-GM grain counterparts.

Palatability of SCP sources has shown some variability, with responses from the various SCP types reported from being relatively benign to strongly negative (Glencross et al. 2020b). Early studies examining a *Pseudomonas* bacterial SCP at up to 45% inclusion reported that at each inclusion level the SCP resulted in poorer feed intake by rainbow trout (Matty and Smith 1978). An examination of the application of an *Methylobacterium* SCP in diets for rainbow trout found that when the SCP was included in diets at 0%, 5% and 10% and used to replace soybean meal, a decline in feed intake was observed (Hardy et al. 2018). And more recently, an evaluation of a *Methylococcus* bacterial SCP at serial inclusion from 0% to 40% reported no impacts on palatability but did include the use of a marine hydrolysate in the formulation to maximize palatability (Glencross et al. 2023). Rajesh et al. (2022) evaluated the dietary potential of a bacterial SCP derived from *Methylococcus capsulatus* in rainbow trout and found that there was a slight reduction in feed intake with high levels dietary SCP with a consequent reduction in growth. Woolley et al. (2023) found this same SCP to be highly palatable to barramundi (*Lates calcarifer*) and Pilmer et al. (2022) reported that yellowtail kingfish (*Seriola lalandi*), fed a diet containing 10% of SCP had a reduction in feed intake. Studies with yeasts have shown that three different genera of yeast SCP (*Candida, Kluyveromyces*, and *Saccharomyces*) reported good utility from each of the resources (Overland et al. 2013). Notably a significant improvement in palatability was observed through the use of the Saccharomyces SCP, whereas the other two SCPs reported relatively benign impacts on feed intake. Microalgal SCPs examined in a study examining the use of *Nannochloropsis, Phaeodactylum* and *Isochrysis* SCP's fed to Atlantic salmon found that inclusion of any of the three SCP (0% 6%, 12% and 24% inclusion) had no negative impacts on feed intake (Skrede et al. 2011). Although other studies have implicated that at an inclusion of 12% of a *Phaeodactylum* SCP resulted in a reduction in feed intake (Sorensen et al. 2016). A study with Tilapia found that the replacement of corn gluten meal by Algamaxx was dose dependent (Hussein et al. 2013). At low levels of replacement (25% replacement of fishmeal) feed intake increased but at higher replacement levels (≥50% replacement of fishmeal) feed intake was negatively impacted, with up to 50% reduction in feed intake.

Digestibility

Once a feed has been consumed, the physiological processes of digestion and absorption constitute the next biggest determinant of value of the feed and constituent ingredients (Glencross 2020). Digestion involves a series of processes acting on ingested feedstuffs necessary to prepare the contained nutrients to be absorbed from the gastrointestinal tract. The digestibility of the nutrients within a feed is a function of the digestibility of its constituent ingredients, and these can vary substantially. Therefore, it is important to formulate feeds on a digestible-nutrient basis, whenever possible. Knowledge of nutrient digestibility is important, not only because of the balance of nutrients available to the cultured animal, but because undigested nutrients within ingested feedstuffs are voided to the culture environment, potentially having adverse environmental impacts.

The amount of public data available on the digestibility of marine protein sources is comparatively scant considering how widespread the use of these ingredients has been across so many aquaculture feeds. Some studies have found that variability in digestibility of fishmeals was subject to the material of origin, though a notable effect of processing was also evident (Anderson et al. 1997). More recent data comparing both forage and by-product resources found that for the most part the digestibility of fishmeals were relatively harmonized now, with forage fishmeals showing near identical characteristics irrespective of origin and by-product fishmeals showing similar, but slightly more variable digestibility attributes (Glencross et al. 2017; Glencross and Bachis 2021).

Among the various types of PAPs, there are both species and processing effects on the digestibility of the various products. In some cases, these effects are quite notable, whereas with other products the variation can be much smaller. Processed mammalian and avian protein sources have been widely assessed for their digestibility in an array of aquaculture species, including rainbow trout, shrimp, silver perch, and barramundi among others (Allan et al. 2000; Bureau et al. 2000; Glencross et al. 2017, 2018). Most PAPs show good protein digestibility characteristics, though this is markedly affected by drying conditions of the material (Rocker et al. 2021). Traditionally, digestibility of blood meals was considered poor, though recent modernization of drying regimes has significantly improved their digestibility (Bureau et al. 2000; Glencross et al. 2017). Similarly, feathermeals also have had mixed reports of digestibility, with some samples being poorly digested, while others being quite good due to differences in processing conditions on the material (Campos et al. 2017; Rocker et al. 2021). The digestibility of insect meals has been reported to be quite similar to fishmeals, again affected by processing conditions (Gasco et al. 2022; Wethasinghe et al. 2022). In a study with Atlantic salmon a 15% inclusion of one of three BSF products: full-fat, partially defatted and partially de-chitinized BSF larval meals replaced a mix of the protein containing ingredients (fishmeal, soy protein concentrate, corn gluten meal) in the diet. Digestibility of the protein in the diet containing the full fat BSF meal was observed to be similar to that of the control diet, but the digestibility of the other diets with the insect meals was marginally lower (Wethasinghe et al. 2022). In European sea bass, digestibility coefficients of five commercially available insect larvae meals depended both on the species considered and the processing method (Basto et al. 2020). A study with rainbow trout by Gasco et al. (2022) reported the digestibility of defatted insect meals made from three different species of insects. The authors noted some distinct differences in protein digestibility among the different species, with the digestibility of individual amino acids similar to that of the crude protein, with the exception of those for cysteine, which were lower. Notably lipid digestibility values were relatively similar irrespective of species.

Protein digestibility of grain proteins has been notoriously variable, with effects due to raw material origin (species) and more notably the level of processing being observed across most grain varieties (Gatlin et al. 2007; Glencross et al. 2020a). Many grain protein resources have considerable levels of carbohydrates which have been shown to cause problems with digestibility by some species (Glencross 2009; Irvin et al. 2016). While starch is often well digested and utilized by some species, other carbohydrates like the non-starch polysaccharides of cellulose and lignin are not well digested by any species (Hemre et al. 2002; Irvin et al. 2016). This abundance of indigestible carbohydrates results in considerable interference with the digestion of the other more nutritionally useful components like the proteins and lipids (Glencross et al. 2008). In addition to the presence of the non-starch polysaccharides, the presence of some antinutritional factors in some varieties of plant ingredients also interferes with the digestibility and necessitates the use of heat treating and/or inclusion of enzymes in the feed to ameliorate the impacts of such antinutritional factors. The development of new feed additives and notably different enzyme preparations is increasingly allowing the improved use of what was once considered non-nutritive content from such ingredients (Castillo and Gatlin 2015). The digestibility of GM grain varieties versus their non-GM counterparts have been observed to show a numerical, but not significant differences in protein and energy digestibility for lupins (Glencross et al. 2003). While evaluations of GM soybean sources had virtually non-existent differences in digestibility of protein, energy and lipid, with the effects of full-fat versus defatted soybean varieties being more influential (Sagstad et al. 2008). The use of fermentation of soybean white flakes was shown by Refstie et al. (2005) to result in numerical, but not statistically significant improvements in protein digestibility. Other studies have observed that fermentation of soybean improves its digestibility of carbohydrates and lipids when fed to rainbow trout (Yamamoto et al. 2010). Improvements in protein digestibility due to the application of a fermentation process relative to the "standard" soybean meal have been reported for several species (Zhuo et al. 2016; Dawood and Koshio 2020). Authors have noted a clear reduction in the protein and peptide size fragments due to the fermentation process with a general improvement in the digestibility of the grains to which it is applied. This effect is suggested to be a response to a combination of effects including the removal of ANF as well as partial degradation of the proteins rendering them more digestible.

Among SCP ingredients both yeast (fungal) and bacterial products have typically been more digestible than most of the microalgal options. Across a range of products examined, the average digestibilities of yeast (80%) and bacterial (86%) products were consistently higher than those reported for microalgal products (76%), though substantial variation has been associated with individual SCP material origins, differences in processing, inclusion levels and acclimation periods used in the evaluation (Glencross et al. 2023). Among bacterial SCP, digestibility is generally consistent across aquaculture species in terms of similar products. For example, the digestibility of a *Methylococcus* SCP when fed to either rainbow trout or Atlantic salmon both resulted in a protein digestibility value of 88% when included in diets at a similar inclusion (Storebakken et al. 1998, 2004; Øverland et al. 2010). Some differences have been observed in the digestibility of *Methyophilus* SCP versus *Methylococcus* SCP (79%-84% vs. 82%-90% respectively), reaffirming the effects of SCP material origins (Kaushik and Luquet 1980; Storebakken et al. 2004; Rajesh et al. 2022). Although the digestibility of bacterial SCP is generally reported as quite high, some work has been undertaken on the use of different processing methods to improve the digestibility of those products. Lysis of bacterial cells *via* autolysis or hydrolysis have both been attempted, but improvements were only noted through autolysis (Schøyen et al. 2005; Agboola et al. 2022). Among the SCP from different yeast species, differences have been observed in protein digestibility (*Candida* > *Kluyveromyces* > *Saccharomyces*) (Vidakovic et al. 2019). In other studies, there have been no differences at all between *Candida utilize* and *Kluyveromyces,* while *Saccharomyces* SCP was lower (Øverland et al. 2013). In studies on microalgal SCP resources, protein digestibility from both microalgal and yeast SCP products can be improved by specific processing conditions to break the cell walls (Langeland et al. 2016; Shah et al. 2016; Teuling et al. 2017; Batista et al. 2020).

Utilization constraints

Following the absorption of the nutrients from a feed, the capacity of an animal to use those nutrients is fundamentally constrained by the respective balance of the nutrients (and energy) and any inference in the utilization of those nutrients by the presence of anti-nutrients and/or negative nutritional aspects of what has been absorbed (Glencross 2020). The nutritional balance issue is something controlled by the effective formulation of diets, whereas the presence of anti-nutrients and/or negative nutritional aspects are features inherent to ingredients.

Antinutrients

Antinutrients or antinutritional factors (ANF) are natural substances that reduce the ability of dietary nutrients to meet the physiological needs of the animal consuming them. Anti-nutrients are for the most part biologically active substances, that are essentially an evolutionary development of a chemical defence mechanism employed by plants to minimize predation by animals (Francis et al. 2001; Krogdahl et al. 2010; Glencross et al. 2020b). They can act by a range of mechanisms, notably though reducing nutrient digestibility, reducing ingredient palatability or by interfering with the metabolic activity of nutrients and/or cellular function in the animal (Kaushik 1990; Francis et al. 2001). While ANF are generally associated with plants, they can be present in many different types of plant derived ingredients. They are most predominant in legumes, cereals, and oilseeds (Francis et al. 2001). As such, it can be noted that these ingredients make up most of the grain volume used in animal feeds globally. The type of ANF and their concentration within the grain, however, can vary markedly between and within grain varieties (Gatlin et al. 2007; Glencross et al. 2020b; Krogdahl et al. 2022).

Contaminants

Contaminants are another notable negative nutritional aspect that are inherent of all ingredients (Glencross et al. 2020b). Typically, all biological materials, including microbial, plant and animal protein meals (and oils) can suffer from contamination. A wide range of contaminants, including a variety of persistent organic pollutants (POP), such as dioxins, organochlorine pesticides, brominated flame retardants, PCBs, and PFAS, along with certain heavy metals (e.g., As, Cd, Hg, and Pb) can be found in many feed ingredients. What varies among the different ingredients is the type and amount of the various contaminants that are found. Contamination of feed ingredients generally occurs on an unintended basis through the introduction of undesirable environmental contaminants, or during the management of a raw material/crop such with the use of pesticides. Certain ingredients of plant origin are susceptible to contamination by natural toxins such as mycotoxins that are produced by fungi. Residues of each of these various contaminants can occur in protein meals causing a significant reduction in their nutritional value and potentially increasing the risks for negative fish health and/or food safety of humans (Parzefall 2002; Alexander et al. 2012; Gonçalves et al. 2020; Krogdahl et al. 2022). In considering the impacts of the various contaminants on the utilization of an ingredient, the different classes of contaminants often need to be examined from a dose-response perspective, with histological, enzymatic and gene expression effects included to provide greater insights on the involved mechanisms. Additionally, the toxicokinetics of both accumulation and depletion can also be important as it can inform risk assessments on withholding periods or maximum residue levels likely to be accepted (Benford 2013; Silano and Silano 2017).

In terms of managing contaminants, prevention, is always better than remediation. A range of strategies exist to minimize the introduction of contaminants into the food chain, and these are widespread across the global food-production sector but vary in their extent and stringency among different regions and countries. The commonest strategy is based on a monitoring program through the analysis of ingredients to assess both the type and extent of potential risk (Benford 2013; Silano and Silano 2017; Glencross et al. 2020b). The analysis of contaminants is usually underpinned by certain analytical standards that need to be considered to ensure reliability in the results, and these standards and how they are defined vary from country to country (e.g., ISO, AOAC, UKAS etc). Perpetual analytical testing is both cost- and time-prohibitive, so a certain amount of rationalization is applied based on the type of ingredients being assessed and potential risk factors of concern. Once analytical data on the contaminants of concern are obtained, these data are then used to inform about potential thresholds/exposure and the associated risk, so that a risk assessment can be undertaken to better manage the use of any specific ingredient (Parzefall 2002; Alexander et al. 2012). For those contaminants considered major risks of concern, maximum residue levels (MRLs) are determined and define the allowable limits of an ingredient, feed and/or a food product (Alexander et al. 2012; Silano and Silano 2017).

Nutrient damage

The other notable negative nutritional aspects that are sometimes inherent of ingredients is the occurrence of nutrient damage (Glencross et al. 2020b). Nutrient damage is usually based on chemical changes in the qualities of certain nutrients in the ingredient (usually amino acids or fatty acids), often introduced through inappropriate processing of the ingredient, such as excessive temperature and/or inappropriate introduction of moisture or other reactive substances that exacerbate oxidation reactions (Silvan et al. 2006; Estévez 2015). This can occur both at the production of ingredients themselves or during the manufacture of feeds containing the ingredients. Raw materials derived from animal sources usually need to be dried to improve their stability and utility. Heating of a material to dry it is perhaps the most common processing method used to add value to animal-derived ingredients. While heating a substance is useful in reducing the moisture content of a raw material and subsequently improving its microbiological stability, this heating can also impart damage through a range of chemical reactions, including Mailliard reactions, disulfide-linkages and burning of the raw material (Fontaine et al. 2007). Excessive heat during the drying process have been previously linked to a loss of nutritional value from a range of raw materials, often through the loss of certain amino acids through reaction by-products from such Mailliard reactions and disulfide-linkage formation (Plakas et al. 1985, 1988; Bureau et al. 1999; Deng et al. 2005; Glencross et al. 2007; El-Haroun et al. 2009). While damage such as Mailliard products can be measured using chemical assays, assessment of such nutrient damage is often missed during the phenomic assessment steps of ingredient palatability and digestibility and often encountered only during a growth study through the inability of the animal to effectively utilize those damaged nutrients (Fontaine et al. 2007; Glencross et al. 2007).

The SWOT analysis

A SWOT analysis is generally regarded as a type of strategic management technique used to help identify important Strengths, Weaknesses, Opportunities, and Threats related to a particular topic. The technique is designed for use in the preliminary decision-making stages of evaluation and can be used as a tool for considering the strategic position of various options of whatever is being evaluated. As a tool, it is intended to identify the various factors that influence the potential of something achieving its objectives. Strengths and weaknesses are usually considered as internal factors, meaning those factors that are inherently linked to the attributes of the thing being evaluated. Contrasting this, the opportunities and threats are considered as external factors which are those indirectly linked or affected by broader issues of the operating environment or system, such as macroeconomics, sociocultural issues, and peripheral technological developments.

Strengths

The strengths of most ingredients, in terms of a SWOT analysis are those factors that promote their use in feeds and based usually on inherent qualities of the product or its production system. In terms of those inherent qualities, the compositional characteristics of an ingredient are foremost in the mind of a formulator when considering different ingredient options. It can be seen from Table 1a and 1b that the material of origin, has a dominant effect on these characteristics, though a notable effect of processing is also evident. For many feed ingredients, production systems and supply chains are well established, at least in some geographical areas. This only emerges as a strength when considered against those ingredients where such technology readiness level, scale or production systems are not well established. In many a case, feed manufacturing companies need consistency and security of supply and as such niche, low-volume, volatile supply ingredients are not favored.

Marine proteins

When it comes to aquafeeds, marine proteins are still widely regarded for their nutritional qualities and in many contexts, remain the benchmark in terms of feed ingredient qualities. They are rich in protein, with a near ideal balance of essential amino acids and contain a variety of useful micronutrients ranging from long-chain n-3 fatty acids, nucleotides, and bioavailable phosphorus, trace elements and contain no antinutritional factors. Another feature of those benchmark qualities are the palatability features of marine proteins like fishmeals. The inclusion of marine proteins in feeds for most aquaculture species are recognized to enhance the palatability and intake of feeds meaning that inclusion of marine proteins has the ability to offset palatability reductions caused by cheaper, less palatable ingredients (Glencross and Bachis 2021).

Capture fisheries have been the subject of much debate over their sustainability, with many criticisms pointing to the number of unsustainable and overfished fisheries across the world (FAO 2022). Recent data from Hilborn et al. (2022) has demonstrated that small pelagic fisheries, such as those for anchoveta, are among the most sustainable of all global fisheries. As such, it is considered' that their sustainability should be regarded as a strength of marine proteins when adequately managed and monitored. Most fisheries (at least in developed nations) across the world now maintain the capacity to sustain reliable biomass harvests year-on-year because of the implementation of effective fisheries management procedures (Hilborn et al. 2020). It is also worth stating that the greatest beneficiaries of sustainable fisheries are the industry itself. Indeed, significant restructuring of fishing effort toward the end of the twentieth century was required to ensure the maintenance of stock biomasses close to their optimal maximum sustainable yield (MSY), where 'globally' it has now been maintained for almost 20 years (Hilborn et al. 2020). Figures like that from Worm et al. (2006, 2009), once suggested that all fisheries were heading toward extinction by 2048. The turn-around of MSY biomass of most of the world's fisheries is a huge demonstration of the success of good fisheries science and management (Worm et al. 2009; Hilborn et al. 2020). This introduction of modern effective fisheries management has necessitated not only a reduction in fishing effort, but also the introduction of independent stock assessment, quota setting arrangements, fishing zone restrictions, fishing vessel monitoring, among other measures, to ensure the resource use is sustainably managed (Hilborn et al. 2022).

While the high cost and volatility of fishmeal prices were traditionally perceived as a weakness of marine proteins, their price stability in recent years has surpassed that of many other raw materials. Overall price needs to be considered in terms of the nutritional value of the products (usually traded on a profat [protein + fat] basis), so the "high" price of fishmeal is something that can only be considered rationally on a comparative basis (Glencross et al. 2020a). When the ratio of fishmeal price to soybean meal price is examined over the past 20 years (Dec 2002 to Dec 2022) it shows an average ratio of 3.32:1. Prior to June 2020, this ratio was closer to 4:1, but other than the recent decline to 3.3:1, there has been limited volatility in the price ratio since 2014. Prior to this, there was extensive price volatility, with the price ratio peaking at around 5:1 in 2006 and bottoming out at 2:1 in 2012. There are various reasons for this stability in recent years. Notably, improved reliability of fishery yields in dominant producing regions like Peru, is a key factor. In terms of volatility, the monthly price variance of fishmeal and soybean meal, over the past twenty years (December 2002 to December 2022) shows an average of 0.54% for fishmeal and 0.60% for soybean meal [www.indexmundi.com], suggesting that soybean has greater price volatility than fishmeal.

Processed animal proteins

Processed animal proteins have a range of positive attributes that can been seen as strengths. Notable is their widespread availability, with more than 15 million metric tonnes reportedly available globally in 2015 (WRO 2023). Most regions of the world produce PAP of one form or another, with products from poultry, pig and cattle processing dominating production. Even countries with a strong history of consuming animal offal rarely eat by-products like feathers, which are a significant resource with a high-protein content. As by-products from food production, the price of PAP is often quite low, making them quite cost effective on a comparative basis to other ingredients, though specialist PAP products like insect meals tend to not be as cheap, due to their higher costs of production and a poorer ability to offset costs as by-products from food production.

Compositionally, PAP are not dissimilar to marine proteins in that they are often rich protein sources, with similar levels of lipid and ash (Tables 1a and 1b). Blood and feather meals can have very high protein levels (>90%). Insect PAPs generally have lower protein levels (40% to 65%), and markedly higher lipid levels. This richness in protein and lipids provides high nutritional utility to PAP. Processed Animal Proteins are further recognized as having a well-balanced essential amino acid (EAA) profile, with a range of PAP (poultry and insect) shown in Table 1a and 1b. The EAA profile of Dipteran (fly) meals and Coleopteran (beetle) largely depends on the processing applied to each biomass with significant impact on nutrient bioavailability (Basto et al. 2020). The EAA profile of Dipteran meals is quite close to that of a fishmeal; whereas the EAA profile of Coleopteran close to that of soybean (Campos et al. 2017; Basto et al. 2020).

Another recently reported potential strength of PAP is the presence of a prebiotic effect/immunomodulator when porcine blood hydrolysates are used in the diets of European seabass (Resende et al. 2022). The inclusion of as little as 3% blood hydrolysate was found to significantly improve disease resistance in fish.

Grain proteins

The use of grain proteins as feed ingredients has many strengths. Methods for the large-scale production of many varieties of grain products, and the necessary infrastructure and systems are well established throughout the world. The scale of production of these resources dwarfs the other resources by orders of magnitude. This large-scale of production also means scales of economy, with grain products being much less expensive than most other resources (Gatlin et al. 2007).

Most grain protein products are the by-products of human foods, or at the very least co-products where the cost of production is shared with multiple products (e.g., soybean meal and oil are co-products from soybean production). Grain products can be relatively easily processed, and systems are well established to add value to these products to improve their nutritional value (Gatlin et al. 2007). The use of fermentation system to value-add grains is not seen as contentious, and available data indicates that fermentation usually provides some significant enhancement of the nutritional properties of the product (Dawood and Koshio 2020; Zheng et al. 2021; Shi et al. 2022). Grain products store well and have relatively long shelf lives meaning that their value can be maintained over time. Though they are also susceptible to both pest and fungal contamination and special considerations need to be made for their effective storage. The use of grain protein feedstuffs is well accepted in animal feeds, with virtually all animal production systems basing their feeds on such products. As such, the use of grain products is well accepted throughout the world from both a regulatory and social perspectives.

Single cell proteins

Single cell proteins, in the form of bacteria, microalgae and yeasts, provide a strength only shared with grains (plants), in that they allow us to skip trophic levels in terms of nutrient supply. By allowing input from further down the trophic chain, there can be significant efficiencies in the ultimate transfer of nutrients into our food chain. Additionally, production of SCP allows in many cases the potential use of inorganic sources of nutrients (N and C sources being the notable ones), thereby ensuring that protein production from these sources does not compete with potential food production for DHC (Glencross et al. 2020b). This is a distinct strength that SCP have over many grain resources, in that while only plants and bacteria can produce amino acids *de novo* from inorganic N and C sources, grains/plants can be (and are) a major source of direct human nutrition, whereas SCP are not and thus they offer a non-competing nutrient source freeing up many of our planet's limited resources through their production. Estimates also have suggested that it is possible to produce protein at greater potential yields than crops like soybean, but using the same land footprint, whilst still capturing CO_2 and using renewable energy sources (Smetana et al. 2017).

Reports on the composition of many of the SCP are also very favorable (Glencross et al. 2020b). SCPs of bacterial origin have a composition not dissimilar to a high-quality fishmeal (protein around 70% and lipid levels around 10%). Other SCP products have reported protein levels varying from 30% to 80%, depending on source. Microalgal SCP product levels had a reported protein range from 0% to 60%. The protein level though, was dependent on the degree of processing, with lower protein levels often associated with higher lipid levels, or even pure oil products. Fungal (yeast) SCP products had protein levels consistent at between 30% and 60%. The highest protein levels tend to be in the bacterial SCP products, with some products containing protein levels as high as 80% (Glencross et al. 2020b).

Weaknesses

Most ingredients have one or more weaknesses. The notion of a single perfect ingredient should be considered fantasy. Weaknesses are another of what are referred to as the intrinsic factors of ingredients. Weaknesses of ingredients can be of diverse nature: compositional, biological, environmental, economic, or societal which can affect their use in animal feeds.

Marine proteins

Like all ingredients marine proteins have a range of potential weakness in their consideration as ingredients for aquaculture feeds. Of prominence is the environmental non-government organization (eNGO) sector and subsequent public perception that fisheries are unsustainable, with frequent reports and media coverage to this effect (Worm et al. 2006). As mentioned earlier, for marine proteins drawn from dedicated capture fisheries, a range of sustainability and societal issues have been raised (FAO 2022). This perception creates negative pressure on the use of the ingredients in the food-chain. The present perception has established from throughout the later twentieth century arising from the publication of numerous studies reporting declining catches, unsustainable fishing practices, illegal-unreported-and-unregulated activities and ecosystem destruction linked to poor fishing practices (Worm et al. 2006, 2009; Fréon et al. 2014; Cashion et al. 2017). In many respects, the negative perception is not undeserved. As presented in the previous section on strengths, such a situation is no longer the predominant one of modern fisheries, though many fisheries in the developing world continue to be poorly managed (Worm et al. 2009; Hilborn et al. 2020), but like many systems, changes in the broader connotations have yet to filter through to become well recognized and established at global level. There are also various philanthropic funds and institutional entities that maintain a philosophical opposition to the notion of using fish as a feed ingredient and maintain pressure on the sector to change their practices (Packard Foundation 2023; Pew Charitable Trust 2023).

Another weakness of marine proteins is that the sector has limited capacity to increase its volume of production, which has remained relatively stable for over 20 years (FAO, 2022). As has been previously established, the MSY of most forage fisheries is operating at capacity, meaning there is only potential growth if there is growth in the biomass. With by-product resources currently making up about 30% of fishmeal production, there may be some scope for growth from that avenue, but this will be linked to growth in aquaculture production and/or significant investment in the valorization of under-utilized by-product streams from food-grade fisheries. While both options are possible, the overall scope for increased production is likely limited to no more than an additional three million tonnes over the next thirty years as has been suggested (Glencross and Bachis 2021).

Processed animal proteins

Terrestrial animal by-products need processing to be turned into PAP before they can be used. The established rendering systems used to process animal waste streams can generally be categorized according to one of three different approaches: cooking/drying (e.g., poultry offal meal), boiling/drying (e.g., blood meals), or hydrolysing/drying (e.g., feather meals) (WRO 2023). Each of these processing steps serve a range of purposes, notably they breakdown the proteins within the raw materials to increase their utility, but these steps also add costs and possibly affect the inherent nutritional value. Processing also sterilizes the material to some extent, and the drying step improves the long-term stability of the ingredients to enable their use over an extended period. So, while seen as a weakness from a cost perspective, the use of processing does provide some value-added perspectives as well.

The compositional features of PAP can be quite variable. In some cases, this can result in ingredients with significant strengths such as containing very high levels of protein (e.g., feather meals), in others it can mean a critical weakness in comparison to benchmark ingredients like marine proteins, with protein levels being significantly lower and ash levels being very high (>20%). A notable consistent limitation across all PAP though is the lack of long-chain n-3 fatty acids (Marono et al. 2015; Lock et al. 2018). This PAP nutritional value is variable and can depend on a range of things, including species from which the raw material is sourced from, seasonality and regionality (Bureau et al. 1999, 2000). In the case on insects this is a major issue, due to its novelty. Both protein and lipid levels are highly variable, depending on the species, rearing conditions, and processing technologies. Insects often need to be defatted prior inclusion in aquafeeds as high fat contents interfere with the manufacturing process. Although great improvements have recently been reported, this industry still requires to up-scale production, and optimize processing technologies to provide nutritional stable biomass with low fat contents and at a cost-effective price. An inherent weakness with insect PAP is the presence of chitin. Chitin, though it contains nitrogen and therefore can contribute to a falsely high crude protein level, biochemically behaves like a carbohydrate, indigestible to most fish (Basto et al. 2020). Additionally, chitin can be linked to decreased protein digestibility so further processing of insect biomass prior inclusion in aquafeeds might also be required (Marono et al. 2015).

The regionality aspect has further connotations for other weaknesses with PAP. In some countries there is a low social acceptance of the use of terrestrial animal meals in the feed-chain (Glencross et al. 2020a). Reasons for this can be complex, but in some cases are linked to a history of zoonotic threat incidents, like the mad-cow disease outbreak in the United Kingdom in the 1990s, which has led to complete ban on the use of ruminant PAP in the feed-chain not just in the United Kingdom, but also more broadly throughout Europe (European Commission (EC) 2001, 2013). The other low social acceptance perspective is linked to what is colloquially referred to as the "yuck" factor. Sensitivities over perceptions of unnatural products being used in the food chain have been reported to affect consumer sentiment when considering acceptance of farmed fish (Llagostera et al. 2019; Onwezan et al. 2021). A third, social acceptance perspective is linked to religion, with certain religions not allowing the consumption of either or both porcine and blood products either directly or as part of their food-chain.

While most PAP are the by-products of food production systems producing meat for direct human consumption, insects are for the most part not part of such a system. The production of insect meals is based on the cultivation of the animals for use as a feed in their entirety. Though there are also insects being produced as human food, such as the lesser mealworm. It should be noted though, that insects are not a de novo source of protein; in that they too need a source of dietary protein in order to proliferate and grow. As such, insect PAP do not add to the volume of protein available for feed resources. This aspect is a clear weakness of the insect production system. It can be argued though that there is a potential upgrading of the nutritional quality of the protein resource being produced when insects are fed low-grade agricultural or food waste streams, such that in the right context insects can transform unusable protein into usable protein (Wehry et al. 2022).

Grain proteins

The nutritional characteristics of many grain proteins are a significant weakness to their application in aquaculture feeds and this frequently limits their inclusion levels. Amongst the most prominent of the issues here is the poor palatability of grain proteins (Gatlin et al. 2007). Grain protein sources are also notably diverse in their composition, perhaps having the largest variability of all the different ingredient classes being considered, due to the diversity of species and processing options involved (Drew et al. 2007; Gatlin et al. 2007) (Table 1a and 1b). While some grain protein meals, like wheat gluten contain very high levels of protein (>80%), due to the effects of processing, it should be noted that the original cereal grain used to make the product (wheat) typically has a protein level closer to 11% and without this processing, the ingredient has limited value as a protein ingredient (though it does have value as a source of starch)(Glencross et al. 2012). Other grain protein sources like pea and bean meals contain only moderate levels (<30%) of protein. Even soybeans, which underpin the largest volume of feed protein resource on the planet, only has a protein level of ~35%. It too requires substantial processing of dehulling, fat-extraction and for some aquaculture species, additional aqueous extraction is needed to further concentrate the protein. As if the low levels of protein (before processing) were not restrictive enough, the essential amino acid composition of most grain proteins is also limiting in one or more amino acids (NRC, 2011). Without considerable blending of protein sources, or the use of crystalline amino acid additives, the poor amino acid balance of many of the grain protein resources would even further restrict their use (Gatlin et al. 2007).

Lipid levels are also highly variable, being as low as <5% in some grain proteins, like wheat, to being >50% in some oilseed varieties like rapeseed. Most oilseed meals need to be processed (defatted) before they are used in aquaculture feeds as the high fat level can interfere with feed processing, though there are some cases of full fat varieties being used in certain formulations (Samuelsen et al. 2018). Grain protein sources though are most notably distinguished from other ingredients by their high levels of carbohydrates. While some aquaculture species can digest and metabolize carbohydrates when present as starch, virtually none can digest and/or metabolize cellulose, lignin, or other non-starch polysaccharides (Hemre et al. 2002; Irvin et al. 2016; Kaushik et al. 2022). Therefore, this carbohydrate content of grain protein sources is another clear weakness.

A notable weakness of grains is that many contain substantial levels of cellulose, hemi-cellulose, and lignin content (often collectively referred to as non-starch polysaccharides), which for most aquaculture species constitutes non-nutritive content and has little benefit to the diet beyond being a filler (Sinha et al. 2011; Glencross et al. 2020a). Additionally, most grains contain one or more antinutrients or antinutritional factors (Francis et al. 2001; Krogdahl et al. 2010, 2022; Glencross et al. 2020a). Anti-nutrients can act at different levels by impairing nutrient digestibility, reducing ingredient palatability or by interfering with the intermediary metabolism of the animal. Well known and used ingredients like soybeans contain significant levels of many of the known ANF, and extensive levels of processing are used to manage the ANF within them. For example, to ameliorate the ANF in grain proteins, the ingredients often need to be heat-treated, or have enzymes added to deal with them, or require a washing step prior to use. The necessary treatment varying depending on the ANF being dealt with. Another strategy that has long been used for several plant varieties is the use of genetic improvement to produce seeds with reduced levels of ANF. In many cases the production of protein concentrates from grains provides a double benefit of improving the protein level of the ingredient and removing many of the critical ANF in the grain at the same time (Krogdahl et al. 2010).

A final weakness of grain protein sources to consider is their environmental footprint. An increasing number LCA studies and other resource use assessments of many of the various grain products shows that these resources have a high environmental footprint due to extensive need for water, pesticide, herbicide, and energy use in their production (Malcorps et al. 2019). As the environmental footprint of feed ingredients increasingly becomes a consideration in the formulation of feeds, there will be an increased pressure put on grain protein production systems.

Single cell proteins

While some compositional aspects of SCP are strengths, others can be considered as a weakness. A comparison of the crude protein vs sum of amino acids value of many SCP reveals that there is a significant content of non-protein nitrogen in these ingredients (Glencross et al. 2023). A feature of SCP is their relatively high nucleotide content, which being nitrogenous compounds, contributes to the estimation of crude protein. While high levels of dietary nucleotides are problematic for terrestrial vertebrates, aquatic animals appear to have less issue with metabolizing comparatively high levels of these nutrients (Rumsey et al. 1991). Some types of SCP (microalgae) contribute a high level of carbohydrates (alginates), which in some cases can cause complexities with the digestion process in some species. Because of this alginate content, there is a need for considerable processing of microalgae to make them more viable for digestion (Tibbets et al. 2017; Teuling et al. 2019). Studies on the application of different processing techniques indicate that such cell walls in microalgae can be remarkably resilient and can require substantial energy input to break them down (Teuling et al. 2017).

Opportunities

Opportunities for ingredients represent those additional features that add value and encourage their use as an ingredient. While classically, opportunities are meant to be those externalities that influence decisions, some of the opportunities available for some feed ingredients are closely linked to inherent features of the ingredient being considered. In many cases this is subject to the material of origin, though important influences of the types of processing involved in production of certain ingredients are also evident.

Marine proteins

The processing of marine ingredients follows a well-established and understood process of maceration, cooking, pressing, decanting, and drying. This process is relatively amenable to the introduction of additional value-adding steps like the introduction of enzymes or other hydrolytic agents. Because a drying step is mandatory, and the inclusion of a pressing and decanting step already exist, it is a comparatively straightforward process to be able to add further water for such enzyme/hydrolytic mediated value-adding steps. By contrast, grains which are already dry, need to have water added and then a drying step included.

Production of fishmeal and oil from trimmings and by-products is already at a significant scale and far from what would be called "novel". Almost 30% of all fishmeals (~1.4 million metric tonnes) is now coming from various by-product raw material streams (Figure 3). Combined with ~600 thousand tonnes of fish oil produced from by-products, that is close to one third of all marine ingredients currently produced being from "circular" raw material origins. While this momentum behind the use of circular proteins and lipids is clearly growing, further examination of where all this comes from shows aquaculture as now a major player in the provision of fish oils, with both the salmon and pangasius sectors being significant contributors (Glencross and Bachis 2021). On the fishmeal front, while aquaculture is a comparative minor contributor, we note that by-products from human food fisheries contribute 20% of all production, with most of this coming from various pelagic and demersal fisheries. With the growth of aquaculture though, there is a clear opportunity here for growth in the marine ingredients sector. Additionally, as values for fishmeals and oils continue to increase, the by-products from fisheries will increasingly become too valuable to dispose of either at sea or through land-based waste disposal. Increasingly by-catch will become an asset and landings of by-catch may become further mandated by more nations (Regueiro et al. 2022; Newton et al. 2023).

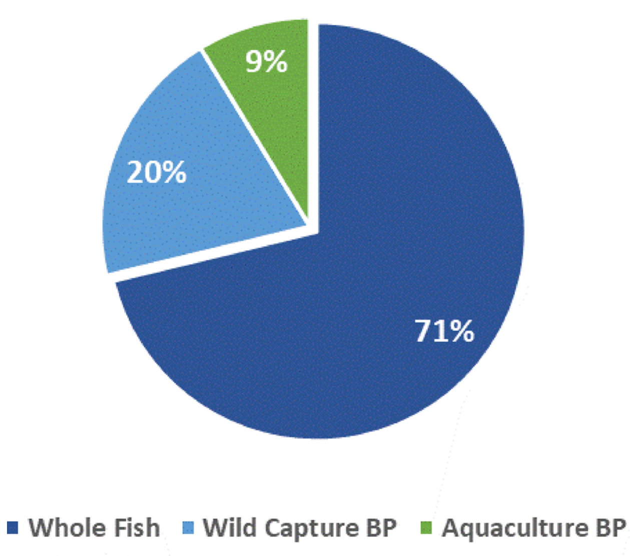

Figure 3. Raw material origins of all global fishmeals in 2020.

The emergence of lifecycle assessment (LCA) analysis as the tool of choice for modern environmental evaluation is helping to reframe the environmental position of marine ingredients in a way that provides several opportunities (Svanes et al. 2011; Cashion et al. 2016; Newton et al. 2023). Lifecycle assessment footprinting characteristics of marine ingredients are among the best of all feed ingredients across many of the 18 different environmental impact categories that LCA encompasses (Newton et al. 2023). The opportunity that the LCA approach presents is the capacity to make sustainability choice management based on a holistic comparison of the full range of environmental effects assignable to different products and services. Lifecycle assessment has a range of advantages in that it provides a framework for the development of a series of holistic sustainability metrics with traceability across the value chain. Arguably just as important is that it allows for greater cross sector harmonization of metrics. For example, the variety of environmental impact categories that LCA examines can be equally applied to fishmeal, soybean meal and insect meal production systems, so that effective direct comparisons between each can be made. Within those impact categories, individual impact categories, such as global warming potential (a.k.a. carbon footprint), can be applied to any feed ingredient, thereby underpinning the basis for the assessment of the full lifecycle impact of feed-production and allow the avoidance of tradeoffs or cross-subsidisations of sectors through incomplete sustainability assessments (Svanes et al. 2011). Notably, the process of undertaking an LCA analysis though requires considerable planning and data, and how you plan and how you collect the data can have important effects on the interpretation and outcomes of an LCA analysis. Because of these constraints, there have been various attempts to set some standards on this; the International Standardization Organization (ISO) initiated this (ISO 14040 series), but for the feed sector the EU have taken a lead with the establishment of the Product Environmental Footprint Categorization Rules (PEFCR) approach (European Commission 2018). More recently the Global Feed Lifecycle-Assessment Institute (GFLI) was established to be an independent repository with freely available database and tools, that also provides overarching guidelines that all who input into the database need to follow [www.gfli.org] (Glencross 2022).

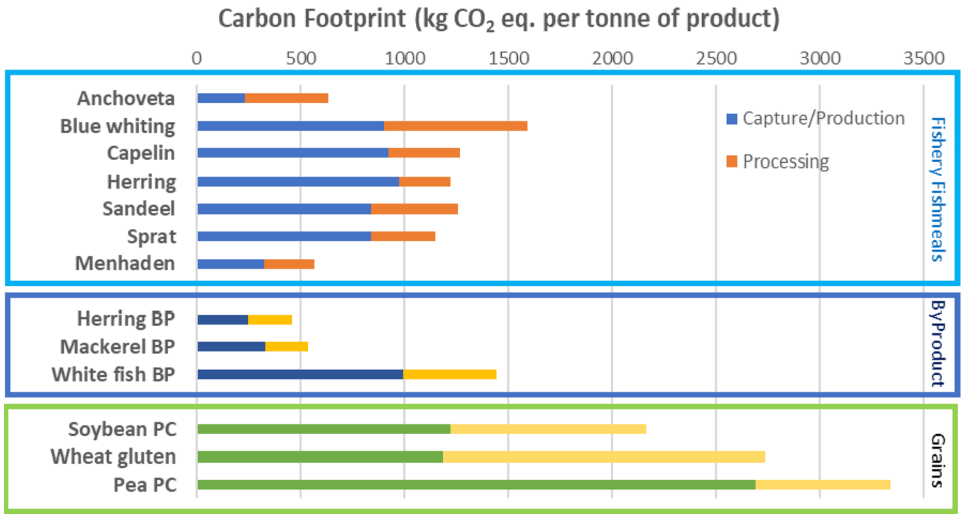

Figure 4. Carbon footprint (as Global warming potential; excluding land use change) of key fishmeal and plant protein concentrate resources (data derived from Newton et al. 2023).

This LCA approach was recently used to present the carbon footprint (and other impact categories) of a range of marine ingredients in a direct comparison against many other traditional feed ingredients (Newton et al. 2023). In this summary of the lifecycle inventories of a wide range of marine ingredients, important alternative ingredients like soybean protein concentrate, wheat gluten and pea protein concentrate were also included (Figure 4), and when compared against various fishmeals, showed that the marine ingredients had very low environmental impacts in global warming potential (carbon footprint), water and land footprints especially. The study shows that all ingredients have strengths and weaknesses, but arguably on balance it shows that the marine ingredients have a lower environmental impact than many of the other presented ingredients, which could be argued as making them more sustainable than the alternatives, although the obvious tradeoff occurs against finite maximum sustainable yields from fisheries and associated processing by-product volumes from various fisheries.

Processed animal proteins

There are various opportunities that are available with the use of PAP as ingredients for aquaculture feeds. Most prominent is the fact that meat consumption globally is growing (Meeker 2006). As animal production for human food increases, so too does the availability of PAP. This provides an increased level of food security in terms of volume of supply. In terms of that volume, for animals like poultry, about 30% of the total biomass of production is available as a by-product that can be processed into a PAP (Murawska et al. 2011).

LCA footprinting characteristics of many PAP are also quite strong. When undertaking a LCA analysis of by-products a spit in the allocation of the production burden between the main (food) product and the by-product is required. While this can be done based on a mass or energy density basis, European Commission PEFCR guidelines mandate the use of an economic allocation method. This allocation of environmental burdens predominantly with the economic allocation, directs most of any environmental footprint to the food part of animal production, leaving only a nominal component directed to the by-product fractions (Svanes et al. 2011; European Commission 2018). Notably, with most LCA footprint analyses of feed ingredients, most of the environmental burden occurs with the production/capture of the biomass. So, if most of that environmental burden is associated with the food product rather than the by-product, then it is largely just the rendering process used to produce the PAP which contributes to its environmental footprint (Campos et al. 2020). Notably there are opportunities to use renewable energy to lessen that impact of the energy used for rendering. This situation would be slightly different for insect PAP though, as they are the main product, with the fras being the by-product and therefore, they would be assigned the majority of the environmental burden associated with their production and rendering, with a further split between meal and oils also needing consideration (Quan Trang et al. 2022).

Further value-addition of various protein sources is also seen as another opportunity during ingredient production. There are commercial supplies now of enzymatically hydrolyzed feathermeals, which have significantly improved nutritional qualities (Campos et al. 2017). Further processing of poultry offal meals has progressed to produce higher value poultry protein concentrates (Simon et al. 2019). With the case of insect PAP production there is strong justification for co-product development with supplementary product streams of insect fats, and purified chitin products (Lock et al. 2018). But value-adding through enzyme/hydrolytic mediated steps may represent a future opportunity to explore functional properties in insect biomass for both feed and food (Nongonierma and FitzGerald 2017).

Grain proteins

The scale of the grain proteins sector provides many opportunities. Processing methods such as fermentation and air classification provide clear mechanism to improve nutritional value of some products, though these are far from the only processing opportunities that have been considered for the value-adding of grain proteins. Grain protein sources also have been the substrate for various fermentation systems being applied, which has the benefit of improving the composition of the product by increasing its positive attributes and reducing some of the negative attributes (like ANF) (Mukerjee et al. 2016; Dawood and Koshio 2020). Processing of plant products to produce co-products from their protein, lipid and carbohydrate fractions have been extensively pursued for almost grain varieties and this opportunity provides a mechanism for defraying the cost of any individual component and increasing the overall value of the resource (Drew et al. 2007).

Both the conventional genetic improvement of plants as well as targeted transgenic approaches have enabled the development and production of several crop varieties with improved nutritional profiles and biological value. While most of the genetically modified (GM) traits associated with grains have directed at improved production capacity traits (e.g., insect or herbicide resistance (Hammond et al. 1996; Brown et al. 2003; Sanden et al. 2006; Hemre et al. 2007; Sissener et al. 2009), there are examples of studies evaluating the utilization of grain-based GM ingredients where a focus on manipulating the product qualities has been the focus, though these tend to be rare for proteinaceous products (Glencross et al. 2003) (Table 2). In what appears to be a unique study with a grain protein fed to an aquaculture species, a GM variety of lupin was modified to include a sunflower albumin gene to enhance the level of methionine in the protein, which was effectively doubled (Molvig et al. 1997). In the feeding study, Glencross et al. (2003) fed the GM lupin to red seabream (*Pagrus auratus*) in a series of studies to determine its digestibility, palatability, and utilization value. Of all the GM grain studies reported there has been only a single trial that has reported any negative effects, with reduced growth related to a mild stress response observed with a corn product (Hemre et al. 2007).

Single cell proteins

Of all organisms where genetic transformation has been involved to modify the genome, the potential application of GM technologies to single cell organisms must be considered the most straight forward (Gressel 2013). This therefore is a massive opportunity for the SCP sector. The opportunities for manipulating the production of the various protein classes to

Table 2. A selection of studies undertaken on the use of genetically modified grain protein ingredients fed to various aquaculture species.

Grain	GM Purpose	Aquaculture Species	Inclusion Level Evaluated (%)	Reported Impacts on Fish	Authors
Corn	Insect resistance (Bacillus toxin gene)	Atlantic salmon (*Salmo salar*)	12.1%	No negative impacts	Sanden et al. 2006
	Insect resistance (Bacillus toxin gene)	Atlantic salmon (*Salmo salar*)	30%	No negative impacts	Hemre et al. 2007
Lupin	Increased production of methionine in seed	Red seabream (*Pagrus auratus*)	30%	Increased level of methionine intake	Glencross et al. 2003
Rapeseed (Canola)	Herbicide tolerance	Rainbow trout (*Oncorhynchus mykiss*)	20%	No difference to parental Canola line	Brown et al. 2003
Soybean	Herbicide tolerance	Channel catfish (*Ictulurus punctatus*)	47.1%	No negative impacts	Hammond et al. 1996
	Herbicide tolerance	Rainbow trout (*Oncorhynchus mykiss*)	31%	No negative impacts	Chainark et al. 2006
	Herbicide tolerance	Atlantic salmon (*Salmo salar*)	12.5%	No negative impacts	Sanden et al. 2006
	Herbicide tolerance	Atlantic salmon (*Salmo salar*)	25%	No nutritional differences between fish fed GM or non-GM	Sissener et al. 2009

improve overall protein yields or improve the balance of essential amino acids or even include additional nutrients like n-3 fatty acids or carotenoids or other bioactive molecules, are all within scope of what could be done using such technologies (Hatlen et al. 2012). In addition to the opportunity for enhancing nutritional qualities of such SCP, the same technological approach could also be used to focus on production efficiency traits to reduce the costs of production.

There are numerous reports of bioactive co-factors being present in SCP products. Whether these constituents are bioactive growth promoters or immunostimulants, or both is a feature that provides clear opportunities for these resources (Romarheim et al. 2013; Sellars et al. 2015), and irrespective they provide a clear point of value addition to the ingredient. While some of these benefits of the SCP ingredients are well known (e.g., n-3 LC-PUFA, nucleotides, or peptidoglycans), for others it remains less well understood (Glencross et al. 2020b). Studies with some SCP products have reported enhancements to immunological, microbiome, and/or inflammatory responses (Romarheim et al. 2013; Sellars et al. 2015). Some SCP products are known to contain relatively high levels of certain immunostimulatory molecules such as nucleotides, peptidoglycans, polyhydroxybutyrate (PHB) and β-glucans (Glencross et al. 2020b). Therefore, the inclusion of these SCP products in feeds contributes these accessory molecules in addition to their protein content. In some cases, SCP products have been secondarily processed to concentrate the bioactive components to potentiate their impact (Romarheim et al. 2011, 2013; Sellars et al. 2015). Use of the *Methylococcus* bacterial SCP was shown to reduce the enteritis in Atlantic salmon caused by dietary soybean meal (Romarheim et al. 2011, 2013). With further processing of the SCP products to increase the concentration of their bioactive molecules there are additional opportunities to produce lower-cost co-products rich in protein and differentiate nutrients from bioactive products in the marketplace (Gamboa-Delgado and Márquez-Reyes 2018). A co-product approach to production has been used widely in the plant product processing sector to help reduce the overall costs of production of each co-product (Cohen and Ratledge 2015).

The inclusion of simple value-adding steps (e.g., such as the use of enzymes) is a comparatively easy and straightforward opportunity for SCP production technologies using fermentation style systems. As an example, the use of autolysis as a production step has been shown to have the capacity to improve the nutritional qualities of SCP products for limited additional cost.

Threats

The threats class of the SWOT analysis perhaps has the clearest link to externalities in the ingredient evaluation process. The threat class is something that impacts the potential of an ingredient to deliver its nutritional value, be that directly or indirectly. These might be global external factors like climate change, or macroeconomic factors bigger than the feed sector alone. These are the factors that have the potential to derail progress despite best management attempts.

Marine proteins

With the main source of raw material for marine ingredients being from fisheries around the world, the growing specter of climate change has been identified as one of the greatest threats to not just fisheries, but entire marine ecosystems. Halpern et al. (2019) examined the cumulative impact related to 14 different environmental stressors (e.g., climate change, fishing, terrestrial pollution, etc) and how these impacted 21 different types of marine ecosystem over the period 2003 to 2013. The results of the study provided clear perspective about the realities of human impact on marine ecosystems. Notably the authors found almost 60% of the world's oceans are facing increasing (and cumulative) human impacts on each of the different ecosystems included in the study. What was noted was that climate change factors induced nearly all the observed changes in the models. Interestingly, there was almost zero impact associated with any of six different forms of fishing activity included as potential environmental threats in the model. The main threats being those of sea surface temperature and sea-level rise changes.

The occurrence of illegal, unreported, and unregulated (IUU) fishing is another significant threat to the sustainable supply of fishery resources. In 2020 we note that about 30% of global fishmeal production (~1.4 million metric tonnes) came from by-products from fish caught or grown for direct human consumption (Glencross and Bachis 2021). This means that, using the industry standard yield of 22.5%, about 6.2 Mtonnes of fish by-products were used to underpin that production. Any threat to the sustained supply of that production would therefore likely impact marine ingredient production. Notable species considered in that list of fish supplying by-products into the marine ingredient sector include various tunas, cod, Alaskan pollock, Atlantic herring and Atlantic mackerel among others; each of these being well known and utilized fish from well-established wild fisheries. It should be noted that the IUU threat is one that almost exclusively is based on higher-value food species, not forage fish. The landed value of forage fish usually being so low as to not warrant the risks associated with IUU activities.

Poor fisheries management is another potential threat, and this one could affect both food and forage fisheries (Worm et al. 2006; Hilborn et al. 2020; Zhang et al. 2020). Presently only ~3.5 million metric tonnes of fishmeal come from forage (reduction) fisheries. That means about 15 million metric tonnes of fish is harvested each year (using the industry standard yield of 22.5%) to produce that fishmeal. From those 15 million metric tonnes, a review of the FishSource Scores data on reduction fisheries from the eNGO Sustainable Fisheries Partnership (SFP) [https://sustainablefish.org/], shows that the 24 main global stocks used for reduction purposes in 2019 accounted for about 10 million metric tonnes of harvested fish. Of those 24 fisheries assessed, more than 79% of the volume was deemed to have come from well managed fisheries. Notably, of the remaining 21% of those 10 million metric tonnes, the loss of the Marine Stewardship Council (MSC) sustainable fishery certification from the north Atlantic Blue whiting fishery meant that this could have been 94% of the fish being from well managed fisheries had this certification not been lost. This MSC certification was rescinded in 2020 due to a lack of agreement amongst the relevant coastal states in the North Sea on fishing quotas. As can be seen from the Blue Whiting situation, often this is more a political issue, and less so a fisheries management issue. This last point demonstrates a further threat in the sourcing of sustainable marine ingredients, that being political instability and/or indecision. Political instability or ineffective political management can also threaten agreed stock sharing arrangements between nations with shared resources.

There are some regulatory constraints (threats) that exist with the use of marine proteins, mostly linked to the use of antioxidants in the products. Antioxidants are required to avoid spoilage of the long-chain n-3 abundant in marine proteins, but there is also a risk of spontaneous combustion of these ingredients under certain conditions and a minimum level of antioxidant inclusion is mandated to be included in the meal at the time of shipping to avoid combustion (IMO 2023). The conditions governing shipping risk are determined by the International Maritime Organization (IMO). Other regulatory conditions imposed in marine proteins are around food safety regulations regarding the maximum levels (MRL) of antioxidants in the product. These regulations in Europe are set by the European Commission (EC), based on an opinion provided by the European Food Safety Authority (EFSA). Other regulations are imposed on the levels of various contaminants (heavy metals and persistent organic pollutants), with MRL set by both the EC and CODEX (EFSA 2005).

Processed animal proteins

The existence of strong legislation in some regions to limit the capacity of the feed sector to use certain PAPs has been a significant threat (European Commission (EC) 2001, 2013). The introduction of legislation over 20 years ago in Europe to prevent, control and eradicate the potential transfer of transmissible spongiform encephalopathies (TSE) remain as some of the strictest biosecurity-based regulations impacting the feed sector (European Commission (EC) 2013). While the earliest forms of these regulations had a partial repeal in 2014 (EC 187/2014) to permit the use of avian and porcine by-products, the ban on the use of any ruminant meals in Europe remains (EC 56/2013). Notably, outside Europe there are few restrictions governing the use of ruminant or other land animal meals in aquaculture feeds, and in South America, Asia, and Australasia there continues to be widespread use of these products in the aquafeed sector (Bureau et al. 2000; Forster et al. 2003; Williams et al. 2003). Despite changes to the European legislation in 2014, the use of terrestrial animal proteins remains limited (Gasco et al. 2020). If TSE were to occur in other regions beyond Europe, then the further introduction of regulatory controls may be something to be expected.

Another threat that has been reported is the adulteration of PAPs (and marine proteins) with lower quality products (Murray et al. 2001; Kong et al. 2022; Zhang et al. 2020). This practice, though rare poses a significant threat to the credibility of the sector as a supplier of quality ingredients. There have been efforts to develop methods to check for adulteration using spectroscopy, microscopy or even PCR evaluation methods (Murray et al. 2001). Rendered animal products also have received criticism as being quite variable in their nutritional quality and this variability being one of the key reasons limiting their broader application in aquaculture feeds (Bureau et al. 1999). Causes of this variability include the type of animal species used, what components are included (e.g., whole animal, deboned, bone-in, blood, etc), time since slaughter, storage conditions and temperature at which the components have been kept (e.g., chilled or ambient), cooking temperature during wet rendering stage and the type of drying technology used. Each of these factors in the rendering process can affect the nutrient composition and digestibility of resultant products (Bureau et al. 1999; Glencross et al. 2017, 2018).

A final potential threat to production of PAP is the energy costs associated with rendering and drying the products (Meeker 2006). As energy costs rise, the price differential between the value of the PAP as a feed ingredient, versus its value as a biomass in energy generation begins to narrow. Notably, many PAP trade at a significant discount to other proteins like fishmeals making them sometimes marginal in term of their production value if energy costs increase too high.

Grain proteins

Arguably the greatest threat facing grain protein production is that of climate change (Lobell et al. 2011). Reviews of the impacts of various climate change scenarios on grain production across the world have indicated that this represents a significant and growing challenge (Lobell and Gourdji 2012; Asseng et al. 2015). Many grain production areas are already in climatic areas where a reduction in rainfall can push production from being viable to non-viable (John et al. 2005; Fraser et al. 2011). Some other regions are likely to see increasing levels of humidity, which increases the risks associated with mycotoxin contamination (Gonçalves et al. 2020). In many cases it is the growing uncertainty of the severity of climate change that causes much of the problem in that it limits the ability of producers to effectively manage the risk associated with grain production. While in some instances grain production is reliant on irrigation system for its production, this use of freshwater resources is also increasingly coming under scrutiny for environmental, economic and climate change reasons.

Another threat facing grain production is that of the demands for food by a growing world population (FAO 2022). Current estimates on the global population predict a further rise of between 0.5 and 2.5 billion people over the next 50 years. As the world population continues to grow there will be increasing competition between the use of grains for food-feed-fuel. In the mid-2000s the push by the developed world toward producing biodiesel and bioethanol placed a notable pressure on global grain prices (Wright 2014). The balance between supply and demand for grains has historically been one of agriculture's notable success stories, with growth in grain production generally closely tracking growth in grain demand. With recent rising fuel and commodity prices due to a range of factors, the exposure of the grain sector to such price sensitivity and volatility has reemerged as a key factor in the utility of many grain resources as feed materials. The introduction of additional competition in the form of fuel demands, the occurrence of geopolitical conflicts that constrain access to key grain producing regions for international trade, and the advent of major disruptions to global supply chains due to shortages in logistics can easily compound to cause major imbalances to feed/food production chains.

A final threat, specific to fermented grain production, as with processing of all wet products, is the energy costs associated with drying the products (Hnin et al. 2018). With plant-derived products, inadequate drying not only has energy cost issues associated with it, but also the risk of introducing fungal contamination and the introduction of mycotoxins (Gonçalves et al. 2020). As such the need to ensure adequate drying of such fermented grains is a clear threat.

Single cell proteins

Major threats to the viable establishment of SCP production are its cost and scalability (Jones et al. 2020). As such the main industrial constraints (threats) to the development of SCP are more economic, and less so technical ones. All ingredients, have critical price points at which they compete, and such values can be easily determined using a shadow-costing approach (Glencross et al. 2020a). There are a range of variables that can affect that price point, and it can also be manipulated to a certain extent by adding secondary points-of-value, such as through the demonstration of valuable points-of-difference on criteria like animal health or product qualities (Glencross et al. 2020b). Further processing of the SCP to concentrate nutritional characteristics is another way of accentuating this value, though such processing usually come with additional costs and yield discounts (Chua and Schenk 2017; Soto-Sierra et al. 2018). Another perspective to this equation though is the reduction in the cost of production. Therefore, further refinement of production systems and strategies for increasing scale and improving cost efficiency are likely to be helpful in addressing this threat. Many of these issues related to the current TRL that the sector is placed at, where it still needs to develop further. The use of capital-intensive fermentation systems allows significant control over the production process for these resources, but clearly requires a large up-front capital investment. The need for critical inputs into the process, like the various carbon and/or nitrogen resources (among other things) are likely to add to the costs (both financial and environmental) and there needs to be a continued push to identify ways of reducing those input costs, without compromising qualities and productivity.

Future directions

Based on the current growth trajectory of the aquaculture feed sector there is an urgent need to increase production of feed-grade sources of protein. A crucial point is that they should not compete with the potential to directly feed humans. Grain crops or fish resources that might be fed to animals and may be more effective in food supply if fed directly to humans. Existing resources need to be used more efficiency, and above all we need new resources. This leaves us with but a few options.

Option 1: Improve management of existing resources to increase their productivity. There are several natural resources that currently underpin feed-chains in the aquaculture sector, notably those of fisheries and soil fertility. For fishery resources there is always greater economic gravity to use the fish for direct human consumption, while resources used as forage fisheries are usually only used due to insufficient market demand to absorb all the MSY harvested at a given point in time in a limited geographical area (Fréon et al. 2014; Avadí and Fréon 2015). An important element to that is the management of fisheries (whether they are forage or food), and the setting of what that MSY is in a spatiotemporal dynamic (Hilborn et al. 2020). A key component of this estimation of MSY is the establishment of a total biomass potential of the fishery (Maunder 2002). There also have been arguments that fisheries should be managed to harvest well below their MSY and closer to their maximum economic yield (MEY), to allow for gains in productivity of some fisheries over their longer-term (Hilborn et al. 2020). For grain production, soil fertility underpins the long-term potential of crop productivity. Many current agricultural practices though, result in a systemic loss of soil fertility over time through either organic depletion, loss of essential elements like phosphorus and selenium, and losses due to erosion of high-quality topsoil (Tiessen et al. 1994). Initiatives and changes in agricultural practices like those of no-till farming, and regenerative agriculture are increasingly being seen as essential to help rebuild soil quality across the world (Lal 2015). The extent of these issues though, for both fisheries and agriculture, varies considerably across the world.

Option 2: Irrespective of the resources we produce, ensure we do not waste anything. On reviewing the use of the various protein resources across the world one of the notable things of all the different ingredient classes being considered was that there was nearly always some sector prepared to use them. This occurs because it is becoming increasingly apparent that whatever humans don't eat, gets fed to aquaculture, whatever aquaculture doesn't use gets fed to poultry, whatever poultry does not use gets fed to pigs and so on. While there are arguments for how we better manage our food and feed resources to minimize losses and reduce wastage, the reality is that sometimes the best outcome for a resource is for it to be used to sustain production in a sector that creates a more valued resource through its use as feed. A notable example of this is with aquaculture as a production sector, in that because of the remarkable growth rate that this sector has maintained over years and across the world. Such growth also provides a clear opportunity in that as aquaculture (fish) production grows, so too does the resource base for producing further marine ingredients, albeit from by-products of that food production. While some sectors have already been remarkably successful in recovering valuable nutrients from the non-food by-products of that production, there remains considerable opportunity to improve (Glencross and Bachis 2021). A similar case exists with fishery resources as well. While by-products from fisheries constitute a biomass of some 4.5 million tonnes producing 995 thousand tonnes of fishmeal in 2020 (Glencross and Bachis 2021), this is only a small fraction of the uneaten biomass of the 60 million tonnes of fish harvested annually for human consumption (FAO 2022). Terrestrial animal by-products are another resource that could be much better utilized by the aquaculture feed sector than is currently. Although practices in some parts of the world have well embraced this opportunity (Bureau et al. 2000; Forster et al. 2003; Williams et al. 2003), others lag behind despite the introduction of legislative changes to empower the capacity to use those resource (European Commission (EC) 2001, 2013). Generally, grain products have few by-products that are not utilized, and indeed many protein meals from this sector, like wheat gluten, already end up in the DHC sector and it is only the surplus supply or down-graded products that end up as feed resources (Gatlin et al. 2007). But this use dynamic too represents an important part of the food waste use hierarchy. A growing opportunity in this regard has been the use of agricultural crop residues in the production of insects and SCP as a means to better valorize the use of those resources by turning them into something more useful (Lock et al. 2018; Øverland and Skrede 2017). While the greatest opportunity here lies in the reuse of food and animal wastes, presently legislative restrictions based on biosecurity concerns limit this potential in most of the developed world (EFSA 2015).

Option 3: Further develop non-competing resource production. As noted with option 2, nearly everything already existing has some use, somewhere. Because of this, allocation of say feed grain to aquaculture simply takes that from supply to poultry, that takes that from supply to pigs. This redistribution in effect works to the grain producers' advantage by driving up the price of the grain, but rarely actually adds new material to the overall picture. It is largely a redistribution process of existing production. To actually generate something new to use as feed, what is needed is to consider first that the ultimate objective here is the production of more food. If what is produced is food grade though, then maybe it would be better being used as food to reduce the overall primary demand, and then what "new" feed resources are produced should focus on using noncompetitive resources that are not already part of the food production system. Some clear opportunities here are those ingredients that can be produced from using inorganic or non-food resource bases, things like bacteria, microalgae, and yeasts (Glencross et al. 2020b). Each of these resources has examples of current production where the inputs are from inorganic or non-food resource bases. As such they truly represent new, and non-competing resources in terms of those input demands. As discussed earlier in this review, each of these sectors has a range of techno-economic barriers to address to allow the scale-up to suitable levels where they can become effective contributors to the feed chain (Jones et al. 2020).

This review has examined a variety of considerations that need to be made when examining the use of any ingredient in a formulation for aquaculture feeds. What can be observed is that the science of ingredient assessment is growing from original foundations in the biological assessment space, further into social and environmental science considerations. Collectively, with this evolution a more holistic assessment of the roles that ingredients play in our broader food systems is emerging. As the science progresses in this regard, there will be continuing oversight of regulatory processes to consider, and this too remains a moving target as policy makers continue to demand higher standards in quality and safety.

Disclosure statement

XL has a commercial affiliation with a member-based organization representing the international marine ingredient sector. BG has both a university affiliation and a commercial affiliation with a member-based organization representing the international marine ingredient sector. All other authors have solely a university affiliation and no declared interests.

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