



Alternative protein sources in aquafeed: Current scenario and future perspectives

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ABSTRACT

Fish meal represents the main protein source for most commercially farmed aquatic species, as it is characterized by high nutritional value and lack of anti-nutritional factors. However, its availability and the market price have been recognized as serious problems at least for over a decade, making it necessary to search for non-conventional protein sources, as an alternative to fish meals. This review aims to comprehensively examine and critically revise the use of fish meal and all alternative protein sources explored to date on the health, welfare, and growth performance of the major aquatic species commercially interesting from a global scenario. The investigation revealed that the inclusion levels of the different protein sources, plant- and animal-derived, ranged from 10 to 80 % and from 2 to 100 % respectively, in partial or complete replacement of fish meal, and generated positive effects on health, welfare, growth performance, and fillet quality. However, the results showed that above a certain level of inclusion, each protein source can negatively affect fish growth performance, metabolic activities, and other biological parameters. Moreover, it is likely that by mixing different protein sources, the combination of each ingredient causes a synergistic effect on the nutritional properties. Therefore, the future of aquatic feed formulation is expected to be based on the blend of different protein sources. Overall, the analysis highlighted the need for additional research in the field of replacing fish meals with new protein sources, given that many knowledge gaps are still to be filled on aquatic species, which deserve to be investigated.

1. Introduction

Agricultural production will need to increase by 50 %, to satisfy the growing demand for food according to the expected increase in the global population (9.7 billion people by 2050) (Hunter et al., 2017). Moreover, the increasing consumption of animal-based foods, and the improvement of the living standards in developing countries, will lead to increased global demand for sustainable animal proteins (Kim et al., 2019). For these reasons, alternative feed protein sources will be necessary to replace the current supply and satisfy the growing need. To address this need, research is exploring alternative protein sources for feed, as demonstrated by the increasing number of publications on such topics in the monogastric, ruminant, and aquaculture species in the last 10 years (Fig. 1).

Aquaculture represents one of the most important sources of animal proteins for human nutrition. Fish grow rapidly and provide adequate

calorie-protein ratios for human consumption (Melenchón et al., 2022). Moreover, the increasing demand for seafood, recommended as healthy and sustainable, may be incompatible with ecological sustainability (Teixeira and Silva, 2024). Consumers play a key role, since based on their commercial choices they can promote sustainable fish farming systems, which have now become essential to increase food production as the global population increases.

Many fish reared for human consumption require high protein levels to grow properly, and aquaculture has faced sustainability issues in recent decades. Fish meal (FM) is considered the ideal protein source in aquaculture, particularly for carnivorous species, because it is rich in protein content, properly balanced with essential amino acid (AA) profile, highly nutritive, and palatable. According to the FAO report (2022), 16 million tons of fish caught (9.03 % of the total) are used directly for the production of FM and oil. The rapid growth of the aquaculture sector has significantly contributed to the increasing

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demand for FM, which in turn has led to overfishing and subsequent destruction of aquatic ecosystems (Szczepanski et al., 2022). Total feed production for all fish species is estimated to increase by 75 %, from 49.7 million tons in 2015 to 87.1 million tons in 2025 (Hua et al., 2019). The shortage and the expensiveness of FM have made FM-based feed a limiting factor in the aquaculture industry, leading to the search for alternative sources with high protein content and similar nutritional value (Irm et al., 2022). Ideal alternatives to FM should be characterized by a suitable AA profile, high nutrient digestibility, and low fiber and carbohydrate content. Moreover, the price should be competitive, the environmental impact low, and the source should be fully available, and easy to use. Great efforts have been made to find alternatives to FM and among them are terrestrial plant proteins, animal by-products, insect meals, marine algae, and biomass, characterized by a valuable protein content (Fig. 2) (Aragão et al., 2022). Most likely a combination of different protein sources is better than a single protein source because the mixture has a preferable AA profile, which results in better fish growth performance.

The present review aims to comprehensively examine and discuss the use of FM and all alternative protein sources explored to date on the health, welfare, and growth performance of major aquatic species of commercial interest from a global scenario. This work, evaluating the progress achieved in the last decade, and identifying the most sustainable alternative sources from both economic and environmental views, will help the aquaculture sector to reduce the costs of feed. Finally, possible future approaches based on innovative alternative protein sources not authorized yet, are also suggested.

2. Research methodology

The present review analyses the scientific papers reporting evidence of using alternative feed protein sources in the aquaculture sector. A systematic search of the literature was performed in Minerva (access point to the bibliographic resources available from the University of Milan), PubMed, Google Scholar, Scopus-Elsevier, Scifinder-n, and ResearchGate to retrieve all available studies using the following search terms “alternative protein source”, and “protein feedstuff” followed by the name of the animal species or zootechnical categories (i.e.: fish including *Sparus aurata*, larvae, juvenile, etc.), and “aquaculture”. Specific names of the alternative plant-protein sources (i.e. soybean meal, corn/wheat gluten meal, rapeseed, lupin, etc.); specific names of the alternative animal-protein sources (i.e. blood meal, feather meal,

Hermetia illucens, *Tenebrio molitor*, etc.); specific names of the macro-algae/microalgae, and single-cell protein were also searched in the databases. The review was open to the inclusion of studies written in any language (but with abstract written in English) in the last 10 years reporting *in vivo* studies (on-farm field trials and experimental controlled trials) on the effects of different alternative protein sources on growth performance (improved growth, improved feed conversion ratio, etc.), and studies that evaluated a mixture of other protein sources, also in experimental trials with pathogens (challenge). The search delivered a total of about 350 results. Having removed those results unrelated to the topic, 205 articles were selected.

3. Alternative protein sources to FM

3.1. Plant-protein sourced feedstuffs

Plant protein sources are recognized as the main source to replace FM, due to their wide availability, reasonable cost (Kari et al., 2023), and different AA compositions. A range of plant ingredients are used in the aquaculture industry including grains (wheat, corn etc.), oilseeds (soybean, sunflower, rapeseeds, cottonseed, etc.), and pulses (beans, lupins, peas, etc.) (Obirikorang et al., 2020; Kaiser et al., 2022; Burducea et al., 2022; Szczepański et al., 2022; Reis et al., 2019; Ogello et al., 2017).

Despite these positive features, they show significant limitations; Primarily, the presence of anti-nutritional factors (ANFs; phytate, trypsin inhibitors, and lectins for instance), generally affects palatability and interferes with the efficient nutritional utilization of diets, thus leading to alteration of growth performance, immunity, and lead to inflammation processes (Aragão et al., 2022). No less, it has been reported that ANFs and carbohydrate fractions present in plant-based proteins included in diets may alter the aquatic species' digestion and nutrient utilization (Murashita et al., 2019; Dossou et al., 2021). The use of these protein sources showed contradictory effects on aquatic species. Some studies reported that high levels of dietary plant proteins tend to decrease feed intake (FI) and consequently a worsen growth performance (Sharawy et al., 2016; Kari et al., 2022). Contrarily, several studies demonstrated that FM replacement with plant proteins did not negatively affect the growth performance of animals (Valente et al., 2016), even reporting an improvement (Kari, 2023), reason why it would be desirable to combine different plant proteins to meet the nutritional needs of aquaculture species. In the following paragraphs,

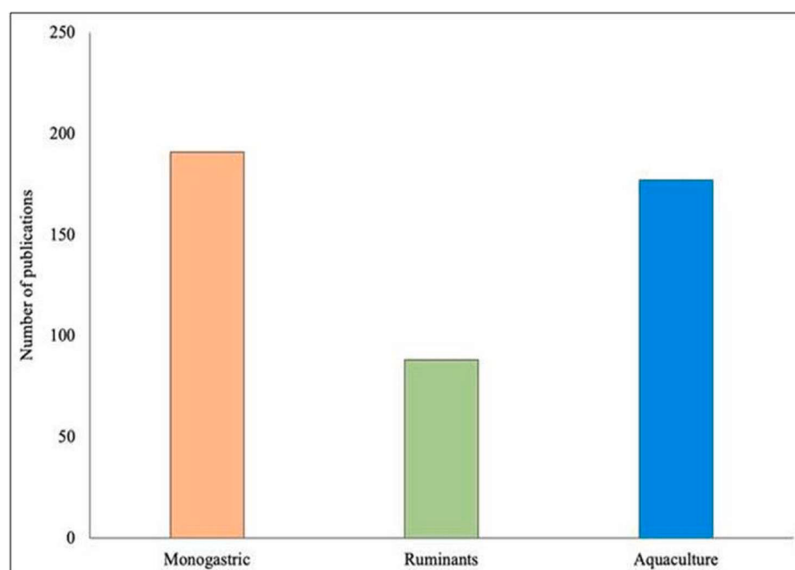


Fig. 1. The number of publications on alternative protein sources in monogastric, ruminants, and aquaculture sectors since 2014.

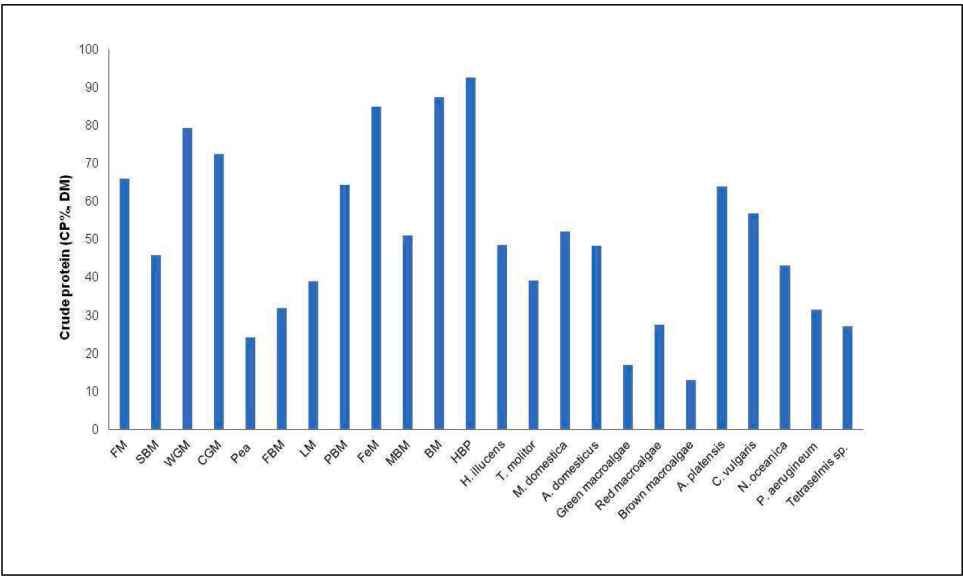


Fig. 2. Protein content (CP %, DM) of suitable alternative protein sources to replace fish meal (FM) in fish diets. FM: fishmeal; SBM: soybean meal; WGM: wheat gluten meal; CGM: corn gluten meal; FBM: faba bean meal; LM: lupin meal; PBM: poultry by-products meal; FeM: feather meal; MBM: meat and bone meal; BM: blood meal; HBP: haemoglobin powder.

the main effects of using different plant-proteins sources used in aquaculture nutrition will be illustrated and discussed. Table 2 summarizes a selection of studies examining the effects of plant-proteins used as FM replacers on key aquaculture species.

3.1.1. Soybean and soybean by-products

Soybean (*Glycine max*, L.) is an annual crop belonging to the Leguminosae family (Dei, 2011). Soybean, and particularly soybean meal (SBM) are the source of plant proteins alternative to FM mostly used in aquafeed. SBM is an excellent source of balanced AAs (Table 1), rich in lysine (Lys), tryptophan (Trp), threonine (Thr), and isoleucine (Ile), which are often scarce in cereal grains (Florou-Paneri et al., 2014). Furthermore, soybean by-products (e.g. fermented SBM, soy pulp, soybean protein concentrate) represent a valuable replacement for FM, due to the lower amount of ANFs generated through the fermentation

process (Zulhisyam et al., 2020) (Fig. 3). Fermentation is a useful technique for removing compounds such as phenols, tannins, and phytates from plant-based feeds, and producing health-promoting biological substances (Kari et al., 2023). Some authors suggest that the microbial fermentation of plant ingredients could enhance the bioavailability of potential antioxidant compounds (e.g. glucosinolates and phenolics) leading to improved anti-oxidative defense in fish (Zhang et al., 2023).

In African catfish (*Clarias gariepinus*) fed with 50 % fermented soy pulp (FSP) in partial substitution of FM, an improvement in growth performance, associated with a significantly lower (desirable) feed conversion ratio (FCR) was observed (Kari et al., 2022). The authors ascribed these results to the lactic acid fermentation that the soybean by-product underwent, with consequent improvement in the nutritional value and elimination of feed allergens and ANFs (Kari et al., 2022). Similar beneficial effects were detected in Japanese seabass (*Lateolabrax*

Table 1
Amino acid profile (% DM) of different plant protein sources used as FM replacement in aquafeed summarized from references.

Amino acid	SBM	CGM	CGM	WGM	PPI	Fava bean	RSM	Untreated <i>L. albus</i>	Fermented <i>L. albus</i>	SFM	CSF
Arginine	3.86	2.01	2.52	2.73	6.3	9.46	2.21	3.29	-	2.24	5.87
Histidine	1.48	1.29	1.19	1.76	1.76	2.41	1.01	0.97	3.13	0.72	1.44
Isoleucine	2.04	2.54	2.35	3.67	3.34	3.94	1.53	1.31	2.44	1.18	1.44
Leucine	3.15	11.36	10.27	5.79	6.26	7.47	2.70	2.4	3.90	1.90	2.80
Lysine	3.19	0.93	1.18	1.38	5.12	7.08	1.95	1.54	5.98	1.07	2.15
Methionine	0.59	1.43	0.60	1.13	0.50	0.87	0.76	0.28	0.83	0.08	0.82
Phenylalanine	2.31	3.59	3.98	4.44	3.47	4.19	1.53	1.24	1.11	1.37	2.64
Threonine	1.76	2.17	2.5	2.13	2.64	3.40	1.76	1.25	6.92	1.10	1.50
Tryptophan	-	-	0.22	0.74	-	0.87	0.51	0.22	-	-	-
Valine	2.11	3.06	2.79	3.71	3.88	4.31	1.97	0.94	4.73	1.42	2.07
Alanine	2.11	5.76	5.80	2.11	2.97	4.15	1.71	1.06	7.85	1.30	1.59
Aspartic acid	5.36	3.83	4.71	-	8.55	10.74	2.83	3.42	5.88	3.12	4.85
Glutamic acid	10.12	19.23	14.22	-	16.73	16.51	6.03	7.05	21.84	6.09	13.75
Glycine	1.91	1.66	1.79	2.76	2.76	4.73	2.01	1.37	6.06	1.72	1.93
Proline	2.15	6.74	-	12.31	3.37	3.94	2.24	1.39	6.05	1.30	1.87
Serine	2.38	3.29	3.38	4.04	3.69	4.69	1.64	1.68	21.98	1.29	2.23
Tyrosine	1.66	3.42	3.40	2.95	2.34	2.78	-	0.915	1.32	0.65	1.44
Cystine	-	1.05	0.62	1.71	0.63	1.33	0.91	0.64	-	0.16	0.94
Reference	Li et al., 2022	Wang et al., 2020a	Santizo-Taan et al., 2020	Kar et al., 2016	Wang et al., 2020a	Martineau-Côté et al., 2022	Mosenthin et al., 2016	Ritter et al., 2022	Krunglevičiūtė et al., 2016	Shi et al., 2023	Wang et al., 2020c

Abbreviations: CSF: cotton seed flour; CGM: corn gluten meal; PPI: pea protein isolate; RSM: rapeseed meal; SBM: soybean meal; SFM: sunflower meal; WGM: wheat gluten meal.

Table 2

Plant-protein sources as a substitute for FM in the diet of different aquatic species.

Alternative protein source	Aquatic species	Inclusion level	FM inclusion in the control diet	Time (weeks)	Effects	Reference
SBM; CGM; SBM + CGM, with or without betaine (B)	Nile tilapia (<i>O. niloticus</i>)	565 g/kg SBM; 565 g/kg SBM + 2 g/kg B (SBM + B); 359 g/kg CGM; 359 g/kg CGM + 2 g/kg B (CGM + B); 106 g/kg CGM + 400 g/kg SBM (CGM + SBM); 106 g/kg CGM + 400 g/kg SBM + 2 g/kg B (CGM + SBM + B)	355 g/kg	8	Performance: highest FBW in CGM+SBM+B; lower FBW in SBM, CGM and CGM+SBM than FM basal diet; Intestinal histomorphology: ↑ intestinal villi length and number of goblet cells in SBM+B, CGM+B, SBM+CGM+B groups; Blood haematology and biochemistry: ↑ HB, blood total protein in CGM+B, SBM+CGM, SBM+CGM+B; highest blood RBCs, WBCs, and globulin in SBM+CGM+B; Gene expression: ↑ LPL and FAS in SBM, CGM, SBM+CGM; ↑ IGF-1 in SBM+B, CGM+B, SBM+CGM+B than SBM or CGM.	Ismail et al., 2020
PCM	Nile tilapia (<i>O. niloticus</i>)	125 g/kg (PCM1); 250 g/kg (PCM2); 375 g/kg (PCM3); 500 g/kg (PCM4)	29 % DM	5	Performance: ↓ in FBW in PCM3 and PCM4; no difference in FCR, FI and ADC of protein; Digestive enzymes activity: no difference in lipase, alkaline protease and amylase activity; no difference in mucosal LYS, ALPR and ALP activities and total IG content; Liver antioxidative status: no difference in CAT, SOD, GPx and MDA; highest gene expression of liver GPx and CAT in PCM4; highest expression of SOD in PCM3; Histology: intensive intestinal and hepatic mononuclear immune cell infiltration, lamina propria expansion and intestinal villus detachment and shortening in PCM3 and PCM4.	Mohammadi et al., 2020
CGM	Rainbow trout (<i>O. mykiss</i>)	9 % CGM; 18 % CGM	16 % DM	24	Performance: no difference in FBW, TCG and FE; Muscle colour: ↓ Astaxanthin isomer, all-trans astaxanthin and all-trans lutein in response to increasing levels of CGM; ↓ Redness (a*) and Chroma (C*ab).	Saez et al., 2016
LM	Rainbow trout (<i>O. mykiss</i>)	150 g/kg LM (LM15); 300 g/kg LM (LM30); 450 g/kg LM (LM45); 600 g/kg LM (LM60)	62 % DM	8	Performance: ↓ FBW in LM45 and LM60; ↓ FI in LM60; Blood parameters: ↓ Hematocrit value in LM30, LM45, LM60; no differences in HB, RBC and MCH rates; no differences in GLU, GOT, GPT; ↓ ALP and LDH in all groups than the control.	Acar et al., 2018
RL; FL	Atlantic salmon (<i>S. salar</i>)	15 % RL (RL15); 15 % FL (FL15); 30 % RL (RL30); 30 % FL (FL30)	562 g/kg	8	Performance: no differences in whole-body composition; ↑ FBW, WG, SGR and PER in FL15; Nutrient apparent digestibility: ↑ ADC of protein and nitrogen-free extract in FL15; Immune response: ↑ LYS activity and leucocyte respiratory burst in FL15.	Rodríguez-Estrada et al., 2020
PPP	Common carp (<i>C. carpio</i>)	10 % PPP (T2); 20 % PPP (T3); 30 % PPP (T4)	-	12	Performance: ↑ WG, ADG and SGR in T3; ↓ FCR in T3	Tewari et al., 2019
CGM	Common carp (<i>C. carpio</i>)	5.4 % CGM (CGM20); 10.8 % CGM (CGM40); 16.2 % CGM (CGM60); 21.6 % CGM (CGM80); 27 % CGM (CGM100)	27 % DM	8	Performance: ↑ FBW in CGM100; ↓ FBW in CGM20; no difference in HSI; no difference in LPV; ↑ PPV in CGM20 than the other groups; Hematological parameters: No difference in RBC number; ↑ CHO level in CGM80; no difference in MCV, MCH, MCHC, GLU.	Potki et al., 2018
RM + <i>Chlorella</i> meal (CM)	Crucian carp (<i>C. auratus gibelio</i>)	99.6 g/kg RM + 99.6 g/kg CM (RCM25); 199.2 g/kg RM + 199.2 g/kg CM (RCM50); 298.8 g/kg RM + 298.8 g/kg CM (RCM75); 398.4 g/kg RM + 398.4 g/kg CM (RCM100)	520 g/kg	6	Performance: ↑ WGR, SGR, FI and PE with increasing RCM inclusion level; Intestinal digestive enzymes: no difference in amylase activity; ↑ trypsin and lipase in RCM75 and RCM100; ADCs: ↑ DM, CP, CL and ash with increasing RCM inclusion level; ↓ ADC values of most AAs in control diet than RCM50, RCM75 and RCM100 diets; Histology of anterior intestine: no significant difference (similar appearance, including intact intestinal mucosal epithelium, well-organized villi, thickness of tunica muscularis and length of villi).	Shi et al., 2017

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Table 2 (continued)

Alternative protein source	Aquatic species	Inclusion level	FM inclusion in the control diet	Time (weeks)	Effects	Reference
CGM	Indian major carps (<i>Catla catla</i> , <i>Labeo rohita</i> , <i>Cirrhinus mrigala</i>)	25 % CGM (CGM1); 35 % CGM (CGM2); 45 % CGM (CGM3)	45 % DM	-	Performance: mean monthly WG highest in CGM3; maximum ADG in <i>Catla catla</i> in all treatments.	Karim and Shoaib (2018)
FBM	“Crispy” grass carp (<i>Ctenopharyngodon idella</i>)	630 g/kg (FBM70); 720 g/kg (FBM80); 810 g/kg (FBM90); 900 g/kg (FBM100)	3 % DM	14	Performance: ↓ FBW, WG, SGR and VSI in all groups than control; Morphology of myofiber: ↑ myofiber area and radius in all groups than control; ↓ myofiber space in all groups than control; mRNA expression: ↑ <i>coll1a1</i> , <i>coll1a2</i> , <i>fgf6a</i> and <i>fgf6b</i> in FBM70 muscle.	Fu et al., 2022
CGM; PBM	Chinook salmon (<i>Oncorhynchus tshawytscha</i>)	59 % fish meal (FM) (HighFM); 15 % FM + 16 % PbM + 28 % CGM (LowFM)	59 % (HighFM); 15 % (LowFM)	56	Performance: no difference in FBW	Doughty et al., 2019
PPC	Juvenile tench (<i>T. tinca</i> L.)	285 g/kg PPC (PPC35); 366 g/kg PPC (PPC45); 487 g/kg PPC (PPC60); 608 g/kg PPC (PPC75); 685.4 g/kg PPC (PPC85)	645 g/kg	13	Performance: no difference in total length and weight; no difference in survival rate; SGR and FCR significantly lower in PPC75 and PPC85.	Carral et al., 2021
CGM	Turbot (<i>Scophthalmus maximus</i>)	212 g/kg (CGM20); 318 g/kg CGM (CGM30); 426 g/kg CGM (CGM40)	620 g/kg	8	Performance: dose-dependent ↓ in growth performance, nutrient digestibility, and feed utilization; Intestinal cytokines: ↑ IL-1β, IL-8, TNF-α and TGF-β gene expression with the rise in the CGM level; Electron microscopic structure of the distal intestine: significantly shorter and less dense microvilli in CGM40; ↑ infiltration of leucocytes from the submucosa to the epithelium layer in CGM40 compared to control; Oxidant and antioxidant indices: ↑ MDA level with the rise in the level of CGM; ↓ SOD, CAT, GPX, GR and GSH levels with the rise in the level of CGM; Intestinal immune parameters: ↓ ACP, C3 and C4, IgM level with the increasing levels of CGM.	Bai et al., 2019
CGM; PPI	Black sea bream (<i>Acanthopagrus schlegelii</i>)	135 g/kg CGM (CGM20); 120 g/kg PPI (PPI20); 70 g/kg CGM + 60 g/kg PPI (CPP20); 270 g/kg CGM (CGM40); 240 g/kg PPI (PPI40); 130 g/kg CGM + 125 g/kg PPI (CPP40)	660 g/kg	8	Performance: ↓ WG of CGM40 than the other treatments; Feed utilization: no difference; Haematological parameters: significantly lower content of serum CHO in CGM40; ↑ liver ALT activity in CGM40 than PPI20.	Wang et al., 2020a
FRM	Sea bream (<i>Pagrus major</i>)	18.75 % (FRM1); 37.5 % (FRM2); 56.25 % (FRM3); 75 % (FRM4)	47 % DM	9	Performance: ↓ FBW, WG, SGR, FI in FRM4; Blood parameters: No difference in GLU, T-Pro, CHO, TG, BUN, T-Bill, GPT; ↓ d-ROMs in FRM1, FRM2 and FRM3; ↑ BAP values in FRM0, FRM1 and FRM2; ↓ CAT in FRM4; Immunological parameters: no effect on serum LYS and total peroxide.	Dossou et al., 2018
LKM	Whiteleg shrimp (<i>Litopenaeus vannamei</i>)	100 g/kg LKM (L10); 200 g/kg LKM (L20); 300 g/kg LKM (L30)	250 g/kg	8	Performance: ↑ FBW in control and L10; ↓ FBW in L30; Haemolymph parameters: ↑ GLU in L10 than L30; no difference in total haemolymph protein; ↓ acylglyceride in L30; ↑ phenoloxidase activity in L10.	Weiss et al., 2020
PPC	Sharpsnout sea bream (<i>Diplodus puntazzo</i>)	160 g/kg (PPC16); 320 g/kg (PPC32); 487 g/kg (PPC48)	550 g/kg	8	Performance: ↓ FBW with increasing PPC inclusion level; no difference in FCR, FI, PER across PPC levels; ↓ HSI in PPC48 compared to control; no difference in PPV and EPV; no difference in AAs composition of muscle; Liver histology: no difference in liver nuclei, liver hepatocyte cytoplasm, hepatocyte vacuolisation or pancreatic acinar cells; Intestine histology: longest villous length in PPC48 (posterior	Nogales-Merida et al., 2016

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Table 2 (continued)

Alternative protein source	Aquatic species	Inclusion level	FM inclusion in the control diet	Time (weeks)	Effects	Reference
					section); widest lamina propria and muscularis thickness in PPC48 (anterior section); greatest villus width in PPC32 (mid intestine).	

Abbreviations: ↑: improvement; ↓: decrease; AAs: amino acids; ACP: acid phosphatase; ADC: apparent digestibility coefficient; ALPR: alkaline protease; BAP: biological antioxidant potential; C3: complement 3; C4: complement 4; CAT: catalase; CGM: Corn gluten meal; CHO: cholesterol; CL: crude lipid; CP: crude protein; d-ROMs: Reactive oxygen metabolites; DM: dry matter; EPV: energy productive value; FAS: fatty acid synthase; FBW: final body weight; FCR: feed conversion ratio; FI: feed intake; FL: fermented lupin; FM: fishmeal; FRM: fermented rapeseed meal; GLU: glucose; GOT: glutamic oxaloacetic transaminase; GPT: glutamic pyruvic transaminase; GPx: glutathione peroxidase; GR: glutathione reductase; GSH: reduced glutathione; HB: haemoglobin; IG: immunoglobulin; IGF: insulin like growth factor; IL-8: interleukin 8; Ile: isoleucine; LDH: lactate dehydrogenase; Leu: leucine; LM: lupin meal; LKM: lupin kernel meal; LPL: lipoprotein lipase; LPV: lipid productive value; LYS: lysozyme; MCHC: mean corpuscular hemoglobin concentration; MCH: mean corpuscular haemoglobin; MCV: mean corpuscular volume; MDA: malondialdehyde; PBM: poultry meal; PCM: processed canola meal; PER: protein efficiency ratio; PPC: pea protein concentrate; PPI: pea protein isolate; PPP: pea pod powder; PPV: protein productive value; RBCs: red blood cells; RL: raw lupin; SBM: soybean meal; SBMIE: soybean meal-induced enteritis; SGR: specific growth rate; SOD: superoxide dismutase; TCG: thermal growth coefficient; T-Bill: total bilirubin; T-Pro: total serum protein; TG: triglyceride; VSI: viscerosomatic index; VW: villous width; WBCs: White blood cells; WG: weight gain; WGR: weight gain ratio.

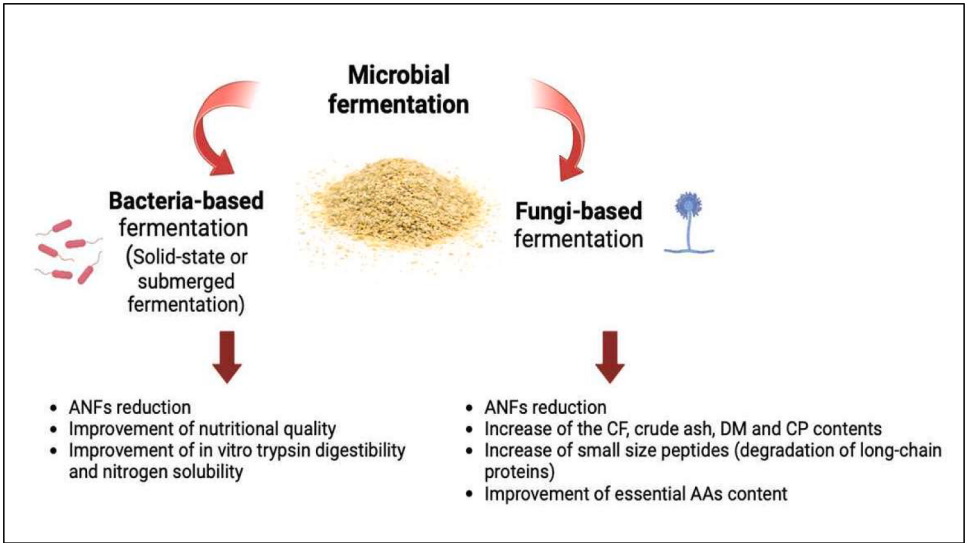


Fig. 3. The fermentation process of soybean meal.

japonicus) fed 40 % fermented SBM, whilst worse growth performance was observed when the percentage of inclusion exceeded 80 % (Rahimnejad et al., 2019). The effects of fermented and un-fermented soybean by-products in the fish diet on growth performance have also been correlated with changes in health parameters, such as immunity, stress, blood biochemical indices, bio-availability of micronutrients, gut morphology, and finally fish fillet composition (Fig. 4).

The partial replacement of FM with fermented SBM or pulp enhanced the innate immunity, along with an increase of lysozyme activity, total antioxidant capacity (TAC), and specific antioxidant enzyme activity (superoxide dismutase-SOD and catalase-CAT) (Rahimnejad et al., 2019; Zhang et al., 2021). Reduced production of the pro-inflammatory cytokines (IL-1 β , IL-6, IL-12, IL-32, and TNF- α) in the intestine and liver (Zhang et al., 2021), and increased expression of genes regulating growth and immunity (TGF- β 1, lyzg, NF-k β , and hsp90 α) were also reported (Kari et al., 2022).

The improvement of the antioxidant capacity and the reduction of inflammatory markers due to the use of soybean by-products can also affect directly the blood biochemical indices (Bonvini et al., 2018). For example, at 75 % FM replacement with SBM, the glucose (Glu) was significantly higher in stinging catfish (*Heteropneustes fossilis*) compared to other treatment groups fed with 0, 18, or 36 % of SBM; this was associated with an increase of BW due to the augmented hemoglobin (Hb), which allowed a better transport of oxygen into the tissues, thus

improving growth rate (Howlader et al., 2023). Commonly, an amelioration in growth performance and positive effects on blood hematology were correlated with an improvement in gut morphology. The above-mentioned study conducted by Howlader and colleagues (2023) demonstrated an increase in the intestinal shape (villi) of stinging catfish by adding SBM up to 50 % in the diet and a decline by adding up to 75 %. In particular, the intestinal villi were increased in length, width, area, and thickness. Moreover, the partial (50 %) replacement of FM with FSP caused positive pathomorphological changes in the African catfish gut, as an intact epithelial barrier with a very well-organized villus structure, *tunica muscularis*, and goblet cell arrangement (Kari et al., 2021). Other authors reported gut disturbances for salmonids (Nimalan et al., 2022), yellowtail (Viana et al., 2019), turbot (Liu et al., 2019), northern snakehead (Miao et al., 2018), and Japanese seabass (Zhang et al., 2018) after the dietary inclusion of SBM at percentages above 10 %, probably due to the presence of ANFs, which cannot be completely removed by the thermal processes. Studies also reported alterations in liver functionality in fish fed soybean by-products, as evidenced by Yaghoubi and colleagues (2016). Silvery-black porgy juveniles (*Sparidentex hasta*) fed with different levels of SBM (0-340 g/kg diet) and isolated soy protein (0-210 g/kg diet), showed liver damage with a marked increase of alkaline phosphatase (ALP) enzymes, but a reduction in plasma alanine aminotransferase (ALT) and aspartate aminotransferase (AST) levels when fermented soybean replaced 20, 40 and 60 g/kg of SBM in the diets

Plant-protein sources	Marine algae
• ↑ CP, moisture, lipid content; ↓ ash content (Howlader et al., 2023; Fu et al., 2022) • ↑ CP and lipid content, ↓ moisture and ash (Karim et al., 2018) • No difference in moisture, CP, lipids, ash contents (Ismail et al., 2020; Saez et al., 2015; Açar et al., 2018; Potki et al., 2018) • No difference in CF (Howlader et al., 2023) • No difference in amino acid composition (Nogales-Merida et al., 2016) • ↓ essential amino acids; no difference in total SFA, MUFA, PUFA (Fu et al., 2022)	• ↑ PUFA (Tomás-Almenar et al., 2018; Guimaraes et al., 2019; Jaseera et al., 2021) • Hypertrophy of the muscle; increase of muscle fiber diameters and higher proportions of larger muscle fibers; ↑ CP, lipids (Knutsen et al., 2018) • ↑ total n-3 fatty acids, DHA, EPA (He et al., 2018; Chen et al., 2019) • ↑ ratio n3:n6 PUFA (Chen et al., 2019) • ↑ MUFA (palmitoleic acid) (Chen et al., 2019) • ↑ skin yellowness (Knutsen et al., 2018) • ↑ skin pigmentation (Ribeiro et al., 2017)
Animal by-products	Insects
• ↓ ash and CP content; no difference in moisture and lipids (Poolsawat et al., 2021) • No difference in moisture, CP, ash (Wang et al., 2020b; Gao et al., 2020; Ding et al., 2020); ↑ lipids (Wang et al., 2020b; Gao et al., 2020); • ↑ moisture, ash, phosphorus; ↓ CP, lipids (Tang et al., 2018) • ↓ CP and lipids (Li et al., 2019) • No difference in moisture, CP, lipids, ash; ↑ SFA, MUFA; ↓ PUFA (Chaklader et al., 2023) • No difference in amino acid profile and lipids; ↑ oleic and linoleic acids; ↑ MUFA (Sabbagh et al., 2019) • ↑ lipids; ↓ ash (Ye et al., 2019) • No difference in moisture and CP (Ye et al., 2019; Nguyen et al., 2023) • ↓ lipids, ↑ ash; ↓ SFA, MUFA, PUFA (Nguyen et al., 2023)	• ↑ DM, lipids; no difference in CP, ash; ↑ SFA, MUFA, PUFA (Caimi et al., 2020) • No difference in DM, CP, lipids, ash (Wang et al., 2017; Belghit et al., 2019; Moutinho et al., 2021; Mastoraki et al., 2020) • ↓ moisture, no difference in skin color parameters (Moutinho et al., 2021) • ↑ SFA, ↓ PUFA (Renna et al., 2017; Moutinho et al., 2021) • ↓ CP, ↑ ash (Coutinho et al., 2021) • ↑ DM, lipids; no difference in CP (Renna et al., 2017) • ↑ rancid odor; no significant flavor differences; ↓ color intensity of the cooked salmon (Belghit et al., 2019)

Fig. 4. Effects of FM alternative protein sources on fillet quality. CP: crude protein; CF: crude fibre; DM: dry matter; DHA: decosahexaenoic acid; EPA: eicosapentaenoic acid; MUFA: monounsaturated fatty acids; PUFA: polyunsaturated fatty acids; SFA: saturated fatty acids.

of largemouth bass (*Micropterus salmoides*) (Jiang et al., 2018).

3.1.2. Corn/wheat gluten meal

Corn gluten meal (CGM), a corn starch by-product, represents the main protein fraction obtained from the wet milling process for the separation of the starch, germ, protein, and fiber corn components. This by-product is characterized by protein content of 67–71 %, low fiber content, and absence of ANFs (Kopparapu et al., 2022); however, is poor in essential AAs such as Lys and Trp (Table 1). Due to its insolubility in water, CGM can be subjected to various physical and chemical processes aimed at increasing its solubility and digestibility and therefore expanding its applications in food and feed industries (Huang et al., 2024) (Fig. 5).

Another by-product rich in protein content (75 %), is represented by

the wheat gluten meal (WGM), obtained after starch extraction from grains. Due to its low Lys content and high digestibility of the protein fraction, it is suitable for use as a feed ingredient in aquatic species (Bonaldo et al., 2015), typically salmonids, whose diet can include WGM in replacement of FM up to 35 % without adverse effects (Storebakken et al., 2000). The replacement of FM up to 30 % with CGM and fermented SBM did not show differences in growth performance and feed utilization in olive flounder (*Paralichthys olivaceus*), with any effects on the immune system (Seong et al., 2018). However, as reported for other plant protein sources, a reduction of the growth rate and feed efficiency was observed with a replacement higher than 80 % of FM with CGM in juvenile spotted rose snapper (*Lutjanus guttatus*) (Hernández et al., 2021). An increasing level of dietary CGM caused a significant reduction in Hb and hematocrit value, with an increase in triacylglyceride levels.

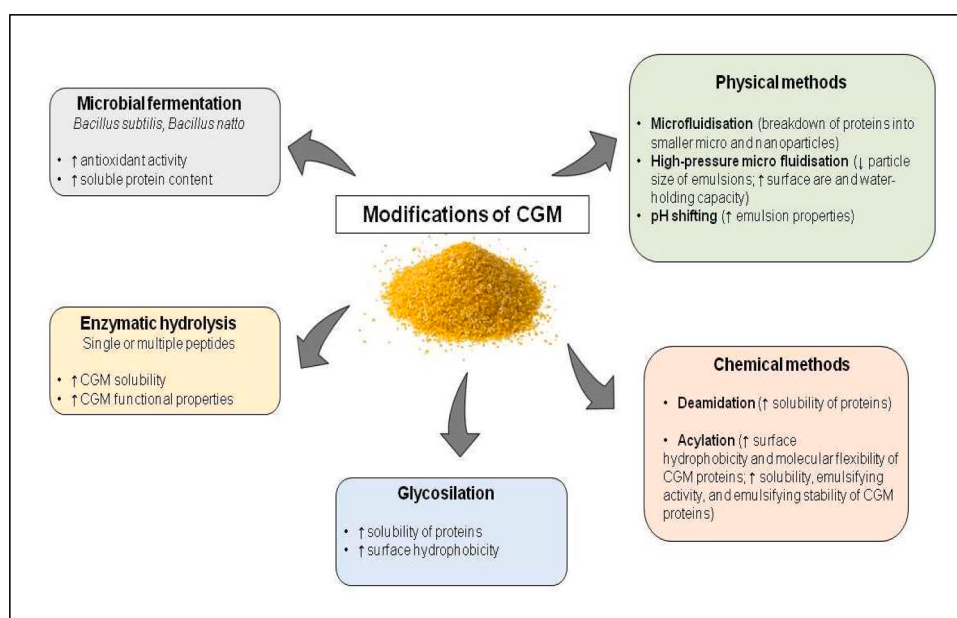


Fig. 5. Different modifications of corn gluten meal (CGM).

These results were explained by an up-regulation of genes involved in the triacyl-glyceride synthesis, similar to the up-regulation of genes involved in lipogenesis in rainbow trout fed gelatinized starch reported by Song and colleagues (2018). Another adverse effect was noticed in Atlantic salmon fed with 30 % WGM, as symptoms similar to gluten sensitivity in humans. This correlated with an up-regulation of cholecystokinin genes, which regulate FI and replacement, and might be caused by a gluten-induced metabolic intestine disorder (Johnny et al., 2020).

3.1.3. Rapeseed and rapeseed by-products

Rapeseed (*Brassica napus*, L.) is one of the most important oil crops in the world, ranking fifth after soy, cotton, peanuts, and sunflower (Lafarga, 2021). It is commonly known as canola (Canadian rapeseed 00 variety) (Kaiser et al., 2022), primarily cultivated for oil extraction, and the meal that remains after this process is a rich source of protein (around 36–50 %) (Thiyam et al., 2004; Muranova et al., 2017). Therefore, it may be used either as a high protein feed supplement especially in cattle, poultry, and aquatic animals, or as organic fertilizer. Rapeseed meal (RM) production has increased steadily over the last few years, making it the second major oilseed meal produced worldwide after SBM (Patrick and Andre, 2014). However, the presence of ANFs (e. g. glucosinolates, erucic acid, tannins, sinnapine, phytic acid, and indigestible carbohydrates) limits its inclusion level as FM replacer in diets usually not above 10–20 % (Sallam et al., 2021). Despite all treatments applied to reduce ANFs and to increase CP content, rapeseed protein products were only sporadically used to replace FM in aquatic feeds without adverse effects on fish's growth performance (Kaiser et al., 2022). To overcome this problem, Kaiser and colleagues (2021) developed processing methods to reduce nitrogen-free extracts as well as ANFs of rapeseed, simultaneously increasing protein content. The resulting highly purified rapeseed protein has been used in diets (66 % replaced of FM) of rainbow trout, without negative effects on growth performance. However, positive effects on growth performance and antioxidant defense (increase in lysozyme, bactericidal, and peroxidase enzymes activities), were evidenced in red sea bream (*Pagrus major*) when fed with FM substituted up to 50 % with different percentages of fermented RM (25, 50, 75, and 100 %), being best 25 % (Dossou et al., 2018).

3.1.4. Lupin (*Lupinus* L.)

Lupin belongs to the Fabaceae family, and the genus *Lupinus* includes 267 botanical species; however, only four of these are cultivated in different pedo-climatic areas, namely white lupin (*L. albus*), blue lupin (*L. angustifolius*), yellow lupin (*L. luteus*), and pearl lupin (*L. mutabilis*) (Abraham et al., 2019). The use of lupin in animal nutrition is not that frequent, due to its low palatability and the presence of ANFs, such as non-starch polysaccharides, oligosaccharides, hemicellulose, cellulose, especially neutral detergent fiber (NDF), and acid detergent fiber (ADF) that affect the nutritional characteristics and reduce the nutrients digestibility (Struti et al., 2020; Parrini et al., 2023). The protein value of lupin is comparable to the ones of SBM, peas, or other legume grains (Sujak et al., 2006), especially after dehulling (De Vries et al., 2012). The lupin's hull represents about 15–30 % of the seed weight, and its mechanical removal contributes to an increase in nutritional value in particular in the level of protein (31.1 and 54.4 % DM). Whole lupine seeds are characterized by a variable AA profile, rich in Leucine (Leu), Valine (Val), Thr, Ile, and Serine (Ser), but poor in Trp and sulfur AAs such as Methionine (Met) and Cystine (Cys) (Table 1).

In aquaculture, the use of lupin as an FM alternative is still under investigation. The few studies available in literature report that a percentage of 75 % of FM replaced with 51 % of lupin meal or a dose of 21 % of lupine kernel meal in Barramundi fish (*Lates calcarifer*) and juvenile cobia (*Rachycentron canadum*) diet respectively, caused liver steatosis, kidney necrosis and gut damage, resulting in worse growth performance (Siddik et al., 2021; Pham et al., 2020). However, some fish species such

as Nile Tilapia (*Oreochromis niloticus*) (Chien and Chiu, 2003), and common carp (Anwar et al., 2020), showed no adverse effects on growth performance, physiological status, and gut integrity when white and blue lupin were added in the diet.

3.1.5. Faba bean (*Vicia faba*, L.)

Faba bean (FB) belongs to the Fabaceae family and is an annual crop cultivated worldwide, sown in autumn or in spring and, even though primarily grown for its edible seeds (beans), also used as a whole crop. FB is an important food and feed legume due to the high nutritional value of its seeds, which are plentiful of proteins (25–33 % DM) and starch (40–48 % DM), thus representing a valuable source of protein and energy for livestock (Guevara Oquendo et al., 2022). Despite being rich in protein, carbohydrates, fats, and minerals, FB seeds contain a variety of ANFs, such as vicine and convicine, well-known to cause the favism syndrome (Rizzello et al., 2016).

In aquaculture, FB diet inclusion at different percentages (40, 50, 60, and 70 %) in Nile Tilapia revealed a decrease in BW proportional to the increase of FB inclusions (Li et al., 2023). However, FB was evaluated as a replacement for SBM. In juvenile grass carp (*Ctenopharyngodon idella*) was demonstrated that FB could be used as a partial substitute for SBM at inclusion levels up to 420 g/kg without affecting the growth performance, whilst a higher inclusion level (560 g/kg) negatively impacted (Gan et al., 2017).

3.1.6. Pea (*Pisum sativum* L.)

Pea belongs to the Fabaceae and Papilionoideae phylogenetic group like soybean (Fischer et al., 2020). Raw peas are relatively low in ANFs compared to dry edible beans, including protease inhibitors, tannins, lectins, and phytate (Iji et al., 2017). Compared to protein-rich soybeans, peas are legumes with relatively lower protein content, which ranges from 18 to 33 % (Walter et al., 2022). Nevertheless, with a lower content of sulfur amino acids and less protein digestibility, pea has a lower nutritional value than, for example, soybeans. Moreover, peas contain more AAs involved in off-flavor development, such as Leu (3.5 vs 6.6 g amino acid/100 g protein for pea and soybean), Ser (2.5 vs 4.8 g/100 g protein for peas and soybean), and Thr (1.6 vs 3.6 g/100 g protein for pea and soybean), making them a less appreciated product (Fischer et al., 2020) (Table 1).

Pea is a common FM replacement for marine and freshwater species. Aside from pea meal, a valuable alternative to FM is represented by pea pods, a food waste of high interest as it is environmentally friendly and able to reduce production costs. Furthermore, pea protein concentrate can be used as an FM protein replacer in fish feed formulation. It was reported that the addition of 20 % pea pod powder in the common carp diet determined higher WG, specific growth rate, and lower FCR, thus demonstrating the efficiency of this by-product in determining better growth performance (Tewari et al., 2019). Also in rainbow trout, lumpfish (*Cyclopterus lumpus*), and tench (*Tinca tinca*), 25 %, 35 %, and 50 % of FM replacement with a pea protein concentrate did not interfere with the fish growth (Demirci et al., 2021; Willora et al., 2020; González-Rodríguez et al., 2016a). However, also in these cases, a higher pea protein inclusion caused harsh histopathological changes in the liver of rainbow trout (Demirci et al., 2021), and affected the growth rate of juvenile tench when the percentage of inclusion was above 35 % probably due to the presence of ANFs (González-Rodríguez et al., 2016a).

3.1.7. Other oilseeds used as fish meal replacer

Sunflower meal (SFM) is a by-product that remains in large quantities after the oil is extracted from sunflower seeds. SFM is a rich source of protein (290–340 g/kg) for fishes, and, due to the price lower than that of SBM and high palatability, it is primarily used as a low-cost protein and energy source for all classes of animals (Banjac et al., 2021; Shi et al., 2023). The content of sulfur-containing AAs in sunflower flour is lower than in SBM, but other AAs are more balanced, especially

glutathione and aspartic acid (Table 1). Using SFM as an FM/SBM replacer has produced good results in different aquatic species. Christopher et al. (2020), obtained an improvement in the growth performance of tilapia when different percentages of SFM (10, 20, and 30 %) were included in the diet in partial substitution of SBM. In particular, optimum growth and feed utilization were observed when SFM was included up to 30 % (best results for FCR, feed efficiency ratio (FER), and specific growth rate (SGR)). In the same aquatic species, SFM was tested as an FM replacer for 210 days at diet inclusion levels from 64.75 to 259 g/kg (Ogello et al., 2017) for growth performance and meat quality of fish. The high growth performance was obtained with the supplementation of 64.75 g/kg SFM (25 % FM replacing), while the reduced growth found when SFM levels were higher could be related to imbalances of dietary AAs such as phenylalanine and methionine and high levels of fiber that limit nutrient bioavailability (Ogello et al., 2017). Regarding the meat quality, the protein content decreased with increasing levels of SFM, probably because of changes in protein synthesis, and different growth rates, while the higher fiber and ash contents were observed in the group fed with the highest SFM level (Ogello et al., 2017). FM could be replaced by SFM at 12.9 % of inclusion, with no significant adverse effects on growth and feed utilization in juvenile turbot (*Scophthal musmaximus* L.), as well as without negative effects on antioxidant parameters (the lowest MDA level and highest TAC, SOD, and CAT activities in fish fed 12.9 % SFM) (Zhou et al., 2016). Similarly, in grass carp (*Ctenopharyngodon idellus*) it was found that the substitution of > 50 % SBM with SFM had significant negative effects on the weight gain ratio (WGR) and FCR of fish (Shi et al., 2023). The incomplete decortication of SFM and the high content of crude fiber and indigestible lignin can reduce the rate of utilization and the nutritional value of raw materials by delaying gastric emptying, so it is advisable to limit high percentages of SFM in diets.

Cottonseed meal (CSM) has been studied as a potential alternative ingredient to both FM and SBM due to its lower cost, and better palatability, although the protein content can be variable (23–53 %) depending on how this product is processed (Hassaan et al., 2019). The imbalance of AAs (Table 1) and the presence of ANF represent the main factors that limit their incorporation into aquatic feed; it is recommended that low levels of CSM be included in the aquafeeds (Kumar et al., 2014). A trial of 90 days performed on South Asian carp (*Catla catla*) investigated the effects of the replacement of SBM with CSM at different percentages (6.25, 12.50, 18.75, and 25 %) on different biological traits (Aslam et al., 2023). According to the results obtained, it was recommended to use a maximum of 50 % CSM as SBM replacement in the diet of *C. catla* to maintain optimal growth performance and other biological parameters, such as antioxidant indices (reduction of MDA and SOD value), intestinal enzyme activity (decrease of amylase, protease, and lipase activity), and intestinal morphology (reduction in the villus height/villus width ratio). Poor nutrient assimilation due to alterations in intestinal morphology may have caused the reduced growth performance observed with high levels of CSM (Aslam et al., 2023). Similarly, the same percentage of FM replacement (50 %) was suggested in the study conducted by Wang et al. (2020c), where different percentages of CSM (8.5, 17 and 25.5 %) were supplemented to red drum (*Sciaenops ocellatus*) diet to partially replace FM and investigate the effects on performance and body composition of fish (Wang et al., 2020c). Results demonstrated that CSF could replace up to 50 % of crude protein provided by FM in diets without significantly affecting growth performance or whole-body composition; conversely, higher dietary levels of CSM decreased weight gain and feed efficiency, probably because of the reduced palatability typical of plant protein feedstuffs (i.e. presence of ANFs such as gossypol in the case of cotton seed) (Wang et al., 2020c). It is worth underlining that red drum appears to have lower sensitivity to the ANFs present in alternative protein sources when compared to other carnivorous fish (Minjarez-Osorio et al., 2016). In Russian sturgeon (*Acipenser gueldenstaedtii*), the inclusion of CSM as FM replacement is more efficient than the inclusion of SBM at both the inclusion rates

tested (19.7 and 39.5 %), as improved the final body weight (FBW) and SGR of fish, together with no adverse effect on serum parameters (i.e. white blood cells, glucose, total protein, and phosphorus) (Emre et al., 2018).

Linseed (*Linum uistatissimum* L.) is a cold-season annual plant, produced in southern Brazil. Linseed meal is obtained after oil extraction as a by-product which has a high protein content (300 g/kg on average). Its high fiber concentration limits its use in aquaculture nutrition since it can compromise the availability and utilization of food nutrients (Pianesso et al., 2020). The production of linseed protein concentrate (LPC) allows the obtainment of a product with higher protein content and reduced ANFs, thus potentially increasing its inclusion in the diets. Given that most of the studies available from the literature on linseed address the use of its oil, considered an alternative lipid source to fish oil, these will not be considered in the context of the present review. In a study conducted on silver catfish, four diets containing different levels (45.8, 91.6, 137.4, and 183.2 g/kg diet) of LPC in partial substitution of FM were tested (Pianesso et al., 2020). The results showed that LPC has FM-equivalent nutritional quality and can replace FM up to 400 g/kg without causing metabolic and histological damage that affects the growth and nutrient utilization of fish. The authors did not report differences in the protein and fat body deposition of the LPC-fed fish, thus demonstrating that this protein source did not interfere with energy metabolism. Likewise, evaluation of the animals' plasma revealed similarities in total protein, albumin, and glucose content, indicating that the nutrients were metabolized without compromising hepatic synthesis. Another linseed by-product is deoiled linseed oil cake (LOC), which contains a high amount of crude protein (34 % dry weight) and for this reason, is a good candidate as an FM substitute. Raw and fermented LOC were tested at different concentrations replacing FM at 10, 20, 30, and 40 % in the diet of rohu (*Labeo rohita*) for 70 days (Banerjee et al., 2023). The results indicated that fermented LOC can replace up to 30 % of FM in rohu diets without compromising the growth and nutrient utilization, as fish fed fermented LOC showed better performance in terms of higher mean WG, SGR, and PER compared with the fish fed diets with the same level of raw LOC; the poor growth of fish fed raw LOC was probably due to AA imbalance and reduced bioavailability of the nutrients as a consequence of ANFs. The carcass composition was influenced by LOC supplementation, as the higher protein deposition was recorded in fish fed fermented LOC. The considerable increase in digestive enzyme activity in fish fed fermented LOC was most likely due to the more efficient utilization of the nutrients than the fish fed with raw LOC. The incorporation of fermented LOC for partial replacement of FM in carp diets should be considered, as it would be cost-effective (much cheaper than FM) and it involves a simple processing technique. Its use should also be evaluated in other aquatic species.

Among pumpkin (*Cucurbita maxima*) by-products is seed cake (PSC), which is produced after the extraction of oil from seeds and is characterized by the richness in protein, fiber, and minerals (Mounes et al., 2024). PSC has proven to be a promising, and cost-effective alternative protein source to SBM for Nile tilapia, as its inclusion at different concentrations (33.5, 67, 100.4, and 133.9 g/kg diet) significantly enhanced growth performance, feed conversion, antioxidant capacity, and immunity (Mounes et al., 2024). In particular, fish fed the diet with the highest PSC inclusion level exhibited the greatest improvements in FBW, BWG, SGR, and FCR, as well as the lower concentration of total cholesterol, triglyceride, ALT, AST, creatinine, and urea, thus demonstrating a hepatoprotective and nephroprotective effect exerted by PSC. The active biomolecules present in PSC may have triggered the antioxidant defense of fish, by increasing the activity of antioxidant enzymes (e.g. CAT, SOD, and GPx) and reducing the MDA lipid oxidation in all PSC-supplemented groups (Mounes et al., 2024). Similar results were obtained from the study by Sezgin and Aydin (2021), who found that increasing levels (126.5, 253, 380 g/kg diet) of PSC in the diets of mirror carp (*Cyprinus carpio*) led to a decrease in both cholesterol and triglyceride levels, with a continued effect on cholesterol until 100 % inclusion

was reached after 63 days of feeding trial. Additionally, fish fed 253 g/kg of PCS in the diet exhibited higher FBW, WG, and SGR than fish fed the control diet (Sezgin and Aydin, 2021). The supplementation of different concentrations (2, 4, 6 g/kg) of pumpkin seed meal (PSM) in Mozambique tilapia (*Oreochromis mossambicus*) for 28 days determined a significant increase in FCR, SGR, FE, and PER (Musthafa et al., 2017). The PSM integration also enhanced the immune response of fish fed 4 and 6 g/kg of *C. mixta*, as the complement activity was significantly increased, and the mortality caused by the pathogen *Aeromonas hydrophila* was reduced in these fish groups than in the control group (Musthafa et al., 2017). Pumpkin seeds and pomace (50 and 100 g/kg diet for both by-products) were included in the Pacific white shrimp diet for 60 days in the study conducted by Zancan et al. (2023). The seeds exerted a negative effect on performance and decreased the antioxidant activity of muscle (< DPPH value), while the pomace improved the growth parameters (better FCR and PER), antioxidant activity, total carotenoid content, and shrimp body color. The improvement in shrimp color, associated with the total carotenoid content, is an important factor in consumer acceptability, making this by-product a sustainable and cost-effective resource for improving the color of this aquatic species (Zancan et al., 2023).

3.2. Non-plant protein sources

3.2.1. Animal by-products

Animal-sourced feedstuffs for aquaculture derive from the by-products of fish, poultry, pork, and beef, as they are made from several organs or tissues, such as blood, intestinal mucosa, feathers, meat, and bone (Jia et al., 2022) (Fig. 6). These animal by-product meals are considered valuable FM alternatives due to their nutritional quality, including an AAs profile more similar to the one present in the animal (Table 3), and low prices. Moreover, they display considerable advantages over plant-derived proteins, such as lack of ANFs. Table 4 summarizes a selection of studies examining the effects of animal-by products used as FM replacer on key aquaculture species.

The Regulation (EC) 1774/2002 (European Union Regulation, 2002) established the definition of three categories of Animal By-products"

(ABPs) (Categories 1, 2, and 3), of which, under European law, only Category 3 by-products may be used to produce processed animal proteins (PAPs) for aquaculture and aquafeed purposes (Reg. EC 1774/2002 (European Union Regulation, 2002).

Poultry by-product meal (PBM), which was re-authorized for use by the European Union in 2013 (European Commission et al., 2013), and is obtained from rendered and clean by-products of the poultry processing industry, and may include head, neck, feet and undeveloped eggs, exclusive of feathers and intestines. The poultry production industry generates large quantities of these by-products, with an annual production of around 175,000 tons of feather meal in Europe (Campos et al., 2017). Despite this, PBM is still sparsely used as a protein source in aquatic feed, although it presents favorable characteristics, such as good palatability and a well-balanced AA profile (Gaudioso et al., 2021). Since most processed animal by-products are characterized by low content in arginine (Arg), Lys, Meth, and Trp, supplementation of these AAs in diets according to fish nutritional requirements, is necessary for the formulation of balanced feeds with essential AAs (Table 3). For example, 30-60 % of diets of PBM in juvenile rainbow trout appeared to represent a valid protein source option in FM-free diets (Gaudioso et al., 2021). Black sea bass and Gilthead seabream fish fed 40-50 % of FM replaced by PBM showed no adverse effects in the growth performance, digestive protease activities (trypsin and chymotrypsin), and hematological and biochemical indices (Dawson et al., 2018; Karapanagiotidis et al., 2019). However, in black sea bass, when FM was replaced 100 % with PBM, the growth was negatively affected. This effect may be due in part to the relatively low dietary levels of essential fatty acids, in particular, the long-chain n-3 PUFAs (Dawson et al., 2018). At the same time, also in other species, such as turbot, negative effects on growth performance and poor FCR were evidenced when fed poultry by-products at high levels (≥ 168 g/kg diet) (Hao et al., 2020). These effects could be due to the accumulation of some toxic substances (e.g. aromatic AA derivatives in the intestinal tract) in poultry by-products, which disrupt digestion and nutrient absorption (Hao et al., 2020).

Among more economically and environmentally sustainable alternative protein sources to reduce production costs is feather meal (FEM), which is becoming attractive due to high supply options, low costs, high

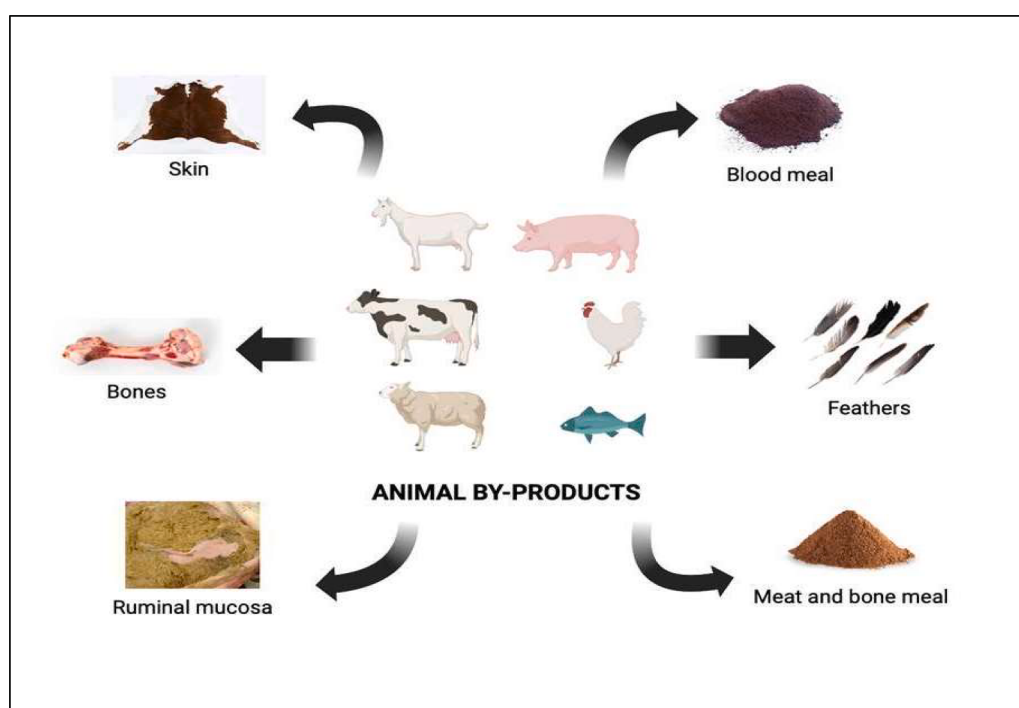


Fig. 6. Main animal by-products used in aquaculture feed formulation.

Table 3

Amino acid profile (% DM) of different animal by-products used as FM replacement summarized from references.

Amino acid	FM	PBM	FEM	MBM	PMM	BM
Arginine	3.75	8.24	5.92	3.44	4.55	4.2
Histidine	1.68	1.10	0.68	1.12	1.47	7.63
Isoleucine	3.13	2.92	4.17	1.76	2.03	0.40
Leucine	5.17	4.48	7.26	3.33	4.3	14.64
Lysine	4.95	3.9	1.85	3.33	3.76	8.75
Methionine	1.97	1.30	0.66	0.86	1.24	0.75
Phenylalanine	2.99	2.21	4.38	1.89	2.35	6.8
Threonine	2.80	2.85	4.01	1.77	2.3	3.14
Tryptophan	-	0.46	-	0.44	-	-
Valine	3.6	3.27	6.63	2.47	2.95	8.45
Alanine	4.14	3.78	3.91	3.93	5.22	8.43
Aspartic acid	6.22	5.30	5.64	3.99	5.12	13.84
Glutamic acid	8.36	5.52	8.86	6.39	8.78	8.34
Glycine	3.72	1.76	6.7	6.36	8.28	4.98
Proline	3.18	4.76	8.81	3.72	5.41	4.05
Serine	2.49	4.23	9.17	1.74	2.7	4.55
Tyrosine	2.20	1.54	2.42	1.39	1.76	2.42
Cystine	0.65	0.65	4.82	0.45	-	-
Reference	Poolsawat et al., 2021	González-Rodríguez et al., 2016b	Poolsawat et al., 2021	Kerr et al., 2019	Huang et al., 2022	Takakuwa et al., 2022

Abbreviations: BM: blood meal; FEM: feather meal; FM: fish meal; MBM: meat bone meal; PBM: Poultry by-product meal; PMM: porcine meat meal

protein content (86 %) and essential AAs, and lack of ANFs (Jasour et al., 2017). Using various rendered animal protein ingredients in combination might be a way to formulate highly nutritive and cost-effective fish feed. This nutritional approach is based on the concept that the nutrient balance and economic cost of a blend of rendered animal protein ingredients are usually better than those of a single ingredient (Wu et al., 2018). Based on this, it was observed that giant croaker (*Nibea japonica*) fish fed a diet with a blend of PBM and FEM to replace FM (20, 40, 60, and 80 %), showed a better final BW, BWG, and FI at percentages of inclusion of 20 and 40 %, compared to the unsupplemented group. In general, it was observed that the FI decreased with the increase in the percentage of FM replaced by PBM and FEM blend, probably due to the negative effect of FEM on palatability (Wu et al., 2018). However, hydrolyzed feather meal (HFM) has been demonstrated to successfully replace FM protein at 25 % without compromising the growth performance, and proximate composition of juvenile gilthead seabream fillet (Psafakis et al., 2020).

Also in this case, as usual, negative effects were noticed with the use of animal blood meal (BM). BM is traditionally produced by heating the liquid blood to ~95 °C to coagulate the blood proteins, which are then separated from the liquid portion by centrifugation. The dietary addition of cow BM over 7 % negatively affected growth performance, feed utilization, and the activity of antioxidant enzymes (CAT, SOD, GPx), with an increase in MDA concentration in African catfish (Ogunji and Ibea-nacho, 2021), while in Nile tilapia the growth performance were negatively affected when BM was included over 50 % (Kirim et al., 2016). Differently, inclusion percentages (2.5, 5.0, 7.5 and 10 %) of other blood by-products such as dried bovine hemoglobin (DBH) (Ibrahim et al., 2022) or spray-dried plasma (16.6, 33.2, 49.7, and 66.3 g/kg) (De Araújo et al., 2017) used to replace FM in the diet of Nile tilapia, showed a linear increase in the growth performance at the level of 10 % of DBH and 51.83 g/kg of dried plasma, respectively. Moreover, an enhancement of the antioxidant hepatic capacity (higher TAC, GPx, and SOD gene expression) was noticed (Ibrahim et al., 2022).

Meat and bone meal (MBM) has high protein content (450-650 g/kg), a well-balanced AA profile, and lacks ANFs (Hodar et al., 2020). MBM has been strictly banned in ruminant nutrition due to the risk of bovine spongiform encephalopathies. Moreover, it has been successfully used for the replacement of FM in the diets of many aquatic animals (Moutinho et al., 2017; Tang et al., 2018; Wang et al., 2020b). The extent of FM substitution by MBM differs markedly between aquatic species, varying for example between 20 and 40 % in olive flounder (*Paralichthys olivaceus*) to 100 % in Nile Tilapia (Lee et al., 2012; Ribeiro et al., 2016). Percentages of MBM of 40.9 or 61.5 % in the gilthead

seabream diet did not affect BWG or feed efficiency up to 61.5 % (Moutinho et al., 2017), but the inclusion percentage of up to 30 % of porcine meat meal (PMM) in juvenile golden pompano (*Trachinotus ovatus*) diet, compromised the activity of plasma antioxidant enzymes, without negative effects on the gut microbiota (Huang et al., 2022).

3.2.2. Insects and invertebrates

Insect farming for the feed industry has increased significantly worldwide (Mulazzani et al., 2021). The European Regulation, 2015/2283 establishes rules for the release of novel foods and has been applied across all European countries since January 2018. Among the so-called novel foods are terrestrial invertebrates, including insects and earthworms. It should be noted that, to date, the use of earthworms as feed for monogastric animals and cattle is not permitted if the earthworms are raised on waste (e.g. animal manure, organic fraction of solid urban waste), despite some preliminary findings proving the safety of this procedure (Conti et al., 2019; Tedesco et al., 2020). In contrast, insect meal (IM) can be used in aquaculture nutrition (European Parliament, 2017).

The insects are a feed ingredient with an interesting nutritional profile, since they are rich in AAs (Table 5), lipids, vitamins, and minerals. Also, the insects are characterized by fast growth and reproduction rates and their requirement of water and land is minimal. For these reasons, the use of insects in fish feed production is considered to be one of the most sustainable and economically viable alternatives (Fisher et al., 2020; Auzins et al., 2024). The frass can also be used as a soil ameliorant (Tedesco et al., 2020; Poveda, 2021; Aragão et al., 2022). For these reasons, the use of insects as a protein source in fish nutrition represents an attractive alternative to FM and has become one of the main focuses of much research over the last years (Nogales-Merida et al., 2019; Alfiko et al., 2022; Tran et al., 2022). Table 6 summarizes a selection of studies examining the effects of different insect species used as FM replacers on key aquaculture species.

The IM is extremely rich in proteins (60-80 %), essential AAs, vitamins, and minerals, and provides a good source of lipids, due to the lipid content of the insects (31-43 %). It must be pointed out that some technological processes such as drying, fat extraction, or enzymatic hydrolysis, can improve the nutritional value of IMs (Mikolajczak et al., 2020). Up to now, several studies have demonstrated the efficiency of IMs in different fish species as FM replacers.

Among insects, the black soldier flies (*Hermetia illucens*) are the most studied for nutrition purposes, followed by the yellow mealworm (*Tenebrio molitor*). The inclusion of black soldier larvae meal in the diet of several fish species has been evaluated at various inclusion levels

Table 4

Animal by-products as a substitute for FM in the diet of different aquatic species.

Alternative protein source	Aquatic species	Inclusion level	FM inclusion in the control diet	Time (weeks)	Effects	Reference
PBM; FEM; LM; MBM	Crayfish (<i>Cherax cainii</i>)	22 % feather meal (FEM); 36.4 % lupin meal (LM); 29.5 % poultry by-product meal (PBM); 24.3 % meat and bone meal (MBM)	30.15 % DM	8	Performance: no difference in % WG, SGR and FCR; ↑ % WG and SGR, lowest FCR (MBM group); survival rate: ↑ in FEM > PBM; lowest survival rate in MBM group; Immune competence: ↑ THC in PBM, differential haemocyte counts increased significantly in FM, FEM, and LM; higher NRRT (FM group); higher PR (FM and MBM groups); Bacterial loads: ↑ in LM.	Saputra et al., 2019
HFM	Pengze crucian carp (<i>Carassius auratus</i> var. Pengze)	2 % (F15); 4 % (F30); 6 % (F45); 8 % (F60)	18 % DM	10	Performance: ↓ FBW, SGR in F60; FE in F30; ↑ HSI in F60; FBW, SGR, HSI of F15, F30 and F45 equal to control group; no difference in FE among F15, F30 and F45; no difference in SR; Antioxidant status: ↓ CAT in F15; ↑ GSH, LPO in F30, F45 and F60; no difference in SOD and GPx; LPO, GSH in F15 equal to control group; no difference in CAT among F30 and F45.	Yu et al., 2020
FEM; EFEM	Tilapia (<i>Oreochromis niloticus</i> × <i>O. aureus</i>)	23 g/kg FEM (FEM50); 46 g/kg FEM (FEM100); 23 g/kg EFEM (EFEM50); 46 g/kg EFEM (EFEM100)	60 g/kg	9	Performance: ↓ WG and ↑ FCR in FEM100 group than control; ↑ VSI in FEM50 and FEM100 than control; ↓ HSI in EFEM50 and EFEM100 than FEM100.	Poolsawat et al., 2021
SDBH	Nile tilapia (<i>Oreochromis niloticus</i>)	2.5 % SDBH (SDBH2.5); 5 % SDBH (SDBH5); 7.5 % SDBH (SDBH7.5); 10 % SDBH (SDBH10)	20 %	10	Performance: increase in FBW, ADWG, TWG, SGR, and PER by SDBH inclusion; Metabolic function indices: ↑ serum growth hormone levels and ↓ serum leptin hormone levels by increasing SDBH level; ↓ serum GLU in SDBH7.5 and SDBH10 groups; Digestive enzymes activity: ↑ amylase and protease by increasing SDBH level; Expression of immune-related genes: ↑ TGF-β, TLR2, and IL-10 (highest expression in SDBH5); Expression of growth-related genes in the muscle: ↑ peptide and AAs transporters, IGF-1, ↓ myostatin in SDBH2.5 and SDBH7.5 groups; Immunological parameters: LYS, NO and C3 levels highest in SDBH5; Intestinal histology: ↑ VH, VW, ratio VH: CD, MCT.	Amer et al., 2022
BM; DPS	Common carp (<i>Cyprinus carpio</i>)	6 % FM (control); 3 % BM (BM); 3 % DPS (DPS); 2 % BM + 2 % DPS (BM+DPS)	6 % DM	12	Performance: No significant difference in FBW, WGR, CF and FCR; Intestinal morphometry: ↓ villus height and fold depth in DPS than FM group; no difference in the muscular thickness.	Gao et al., 2020
MBM	Ussuri catfish (<i>Pseudobagrus ussuriensis</i>)	138 g/kg (MBM20); 276 g/kg (MBM40); 414 g/kg (MBM60); 552 g/kg (MBM80); 690 g/kg (MBM100)	450 g/kg DM	13	Performance: ↓ WG, SGR and FBW in MBM60, MBM80, MBM100M; FCR of MBM80 and MBM100 higher than control; ↓ FI in MBM80 and MBM100; Enzyme activity: ↓ pepsin, intestinal protease and liver protease in all groups; ↓ intestinal lipase with increasing levels of dietary MBM.	Tang et al., 2018
MM; MBM	Ussuri catfish (<i>Pseudobagrus ussuriensis</i>)	91.3 g/kg MM; 84.9 MBM	180 g/kg DM	8	Performance: no difference in FI; ↓ SGR, FE, PER in MBM than control (with FM); ↑ VSI in MM and MBM than control; Digestive enzymes: ↑ lipase intestinal activity in MM; ↓ TAC in MBM than control; ↓ hepatic SOD and CAT than control; ↑ hepatic MDA in MM than control; Expression of IGF-I: no difference.	Wang et al., 2020b
MM	Ussuri catfish (<i>Pseudobagrus ussuriensis</i>)	177.5 g/kg (MM1); 355.1 g/kg (MM2)	280 g/kg DM	8	Performance: ↓ FBW, WG, FI and SGR with increasing dietary MM; ↑ PER in MM diets; Apparent digestibility: No difference in ADC of CP; ↑ ADC of DM, CL and gross energy of M2 than M1 and control; Digestive enzymes: ↑ Pepsin and Alpha-amylase in M2; ↓ Lipase activity with increasing dietary MM levels; Hepatic antioxidant enzyme activity: ↓ TAC and SOD with increasing dietary MM levels; no difference in CAT; Expression of IGF-I: ↓ expression of IGF-I in M2.	Luo et al., 2019
CPP	Largemouth bass (<i>Micropterus salmoides</i>)	38.3 g/kg (CPP50); 76.6 g/kg (CPP100); 115.0 g/kg (CPP150)	510 g/kg DM	12	Performance: ↓ SGR in CPP100 and CPP150; no difference in HSI and CF; ↓ FI in CPP100 and CPP150; ↑ FCR in CPP150; ↑ PER in CPP100; ↓ PRR in CPP150; lowest LRR and ADC of lipid in CPP150; ↓ ADC of essential AAs in CPP150; Immunological and haematological parameters: ↓ serum LYS and respiratory burst in CPP150; ↓ RBCs and HB in CPP150; ↑ haematocrit in CPP50.	Li et al., 2019

(continued on next page)

Table 4 (continued)

Alternative protein source	Aquatic species	Inclusion level	FM inclusion in the control diet	Time (weeks)	Effects	Reference
CHP	Largemouth bass (<i>Micropterus salmoides</i>)	3.83 % (CHP1); 7.66 % (CHP2); 11.50 % (CHP3)	51 % DM	12	Performance: ↓ FI in CHP2 and CHP3; ↓ FER and PER in CHP3; ↑ PRR in CHP1; ↓ ADC of Thr, Met, Leu, Phe, Lys and Arg with inclusion of CHP; Immunological and haematological parameters: ↓ LYS in CHP3; ↓ RBCs and HB content in CHP2 and CHP3; ↓ haematocrit in all groups than control.	Ding et al., 2020
MBM	Climbing perch (<i>Anabas testudineus</i>)	26.35 % MBM (D2); 31.99 % MBM (D3); 37.64 % MBM (D4)	62 % DM	10	Performance: ↓ FBW and WG by FM replacement levels; ↓ FI in D2 > D3 > D4; ↓ PER in D4; Digestibility: ↑ ADC of DM, CP and CL in control diet (with FM).	Hossain et al., 2017
PBM	Gilthead seabream (<i>Sparus aurata</i>)	18 % 36 %	-	16	Performance: ↑ FBW in control diet (with FM); no difference in HSI and VSI; Welfare parameters: No difference in cortisol, protein levels, osmolality, ALT and AST; no difference in liver alkaline phosphatase, lipase and leucine amino peptidase.	Sabbagh et al., 2019
PPH	Gilthead seabream (<i>Sparus aurata</i>)	5 % PPH	7 % DM	13	Performance: ↑ FBW, SGR, FI; no difference in FCR, SR; Antioxidant status: no difference in TAC, SOD, CAT.	Gisbert et al., 2021
PBM; FEM	Giant croaker (<i>Nibea japonica</i>)	87 g/kg PBM + 37 g/kg FEM (B20); 139 g/kg PBM + 59 g/kg FEM (B40); 190 g/kg PBM + 82 g/kg FEM (B60); 242 g/kg PBM + 104 g/kg FEM (B80)	400 g/kg DM	8	Performance: ↑ FBW, WG and FI in control, B20 and B40 than B60 and B80; no difference in FCR and NRE; Waste outputs: No difference in nitrogen waste; ↑ phosphorus waste in B20 and B40 than B60 and B80.	Wu et al., 2018
PBM; SM; BM	Hybrid grouper (<i>Epinephelus fuscoguttatus</i> x <i>Epinephelus lanceolatus</i>)	60.4 g/kg PBM + 73.0 g/kg SM + 10.0 g/kg BM (FM56); 120.9 g/kg PBM + 146.1 g/kg SM + 20.0 g/kg BM (FM42); 181.3 g/kg PBM + 219.1 g/kg SM + 30.0 g/kg BM (FM28); 241.8 g/kg PBM + 292.1 g/kg SM + 40.0 g/kg BM (FM14)	700 g/kg DM	8	Performance: no significant difference in FBW and WG; ↓ FE and PER in FM42, FM28 and FM14; ↑ HSI in FM14; no difference in VSI and CF; Plasma biochemical parameters: ↑ ALT in all diets compared to control; ↑ AST in FM14; ↑ CHO and LDL-C with increasing level of APB; no difference in TG; Liver histology: ↑ occurrence rate of nuclei shifting to the cellular periphery cytoplasmic vacuolization in FM42, FM28 and FM14; Gene expression: ↑ expression of lipid metabolism-related genes (PPARα, CPT1, FAS and apolipoprotein Apo-AI); ↑ expression of apoptosis-related genes (caspase-3, caspase-8, caspase-9 and p53) and inflammation-related genes (IL-8, IL-10 and TGF-β1)	Ye et al., 2019
BM	Red sea bream (<i>Pagrus major</i>)	4.3 % (BM10); 8.63 % (BM20); 12.94 % (BM30)	30 % DM	8	Performance: no difference in FBW, WG, SGR, DFR and SR; Apparent digestibility coefficients: ↓ protein digestibility in BM20 and BM30 than control; ↓ fat digestibility in BM30; Serum analyses: ↑ TP in BM30 than control; ↑ CHO in BM30 than control and BM20; no difference in GLU, TG, GOT and GPT	Takakuwa et al., 2022
MBM; SH	Turbot (<i>Scophthalmus maximus</i> L.)	0 MBM + 45 g/kg SH (MBM0SH); 155.5 g/kg MBM + 0 SH (MBM25); 155.5 MBM + 45 g/kg SH (MBM25SH); 311 g/kg MBM + 0 SH (MBM50); 311 g/kg MBM + 45 g/kg SH (MBM50SH)	470 g/kg DM	8	Performance: ↑ SGR in MBM0SH; ↓ SGR in MBM50; ↑ FCR in MBM50; no difference in FCR among MBM0, MBM0SH, MBM25, and MBM25SH; ↑ FI in fish fed SH; Hematological parameters: ↓ TP in MBM50; ↓ AST in MBM25 and MBM50; ↓ ALT in MBM50.	Nguyen et al., 2023
HFM	European seabass (<i>Dicentrarchus labrax</i>)	5 % (HFM5); 7.5 % (HFM7.5); 12.5 % (HFM12.5)	2.5 % FM Super Prime + 29 % FM60	18	Performance: no difference in FBW, FCR and PER; no difference in final whole-body composition; Digestibility: ↓ protein ADC in HF12.5; ↓ energy ADC in HF12.5; ↑ Phosphorus digestibility concomitantly with the inclusion of HF; no difference in metabolic nitrogen losses; Immune parameters: No difference in peroxidase, LYS, and alternative complement pathway.	Campos et al., 2017

Abbreviations: ↑: improvement; ↓: decrease; AAs: amino acids; ADC: apparent digestibility coefficient; ADWG: average daily weight gain; Apo-AI: apolipoprotein AI; Arg: arginine; AST: aspartate aminotransferase; BM: blood meal; C3: complement 3; CAT: catalase; CD: crypt depth; CF: condition factor; CHO: cholesterol; CHP: chicken haemoglobin powder; CL: crude lipid; CP: crude protein; CPP: chicken plasma powder; CPT1: carnitine palmitoyltransferase 1; DFR: daily feeding rate; DM: dry matter; DPS: dried porcine soluble; EFEM: enzymatic feather meal; FAS: fatty acid synthase; FBW: final body weight; FCR: feed conversion ratio; FE: feed efficiency; FEM: feather meal; FER: feed efficiency ratio; FI: feed intake; FM: fishmeal; GLU: glucose; GOT: glutamic oxaloacetic transaminase; GPT: glutamic pyruvic transaminase; GPx: glutathione peroxidase; GSH: reduced glutathione; HB: haemoglobin; HFM: hydrolysed feather meal; HSI: hepatosomatic index; IGF: insulin like growth factor; IL-8: interleukin 8; IL-10: interleukin 10; LDL-C: low-density lipoprotein cholesterol; Leu: leucine; LM: lupin meal; LPO: lipid peroxidation; LRR: lipid retention rate; LYS: lysozyme; Lys: lysine; MBM: meat and bone meal; MDA: malondialdehyde; Met: methionine; MM: mussel meal; NRE: nitrogen retention efficiency; NRRT: neutral red time retention; PBM: poultry by-product meal; PER: protein efficiency ratio; Phe: phenylalanine; PPARα: peroxisome proliferator-activated receptor alpha; PPH: porcine plasma hydrolysate; PR: phagocytic rate; PRR: protein retention; RBCs: red blood cells; SDBH: spray-dried bovine hemoglobin powder; SGR: specific

growth rate; SH: shrimp hydrolysate; SM: shrimp meal; SOD: superoxide dismutase; SR: survival rate; TGF- β : transforming growth factor-beta; TLR2: Toll-like receptor 2; TWG: total body weight gain; Thr: threonine; VSI: viscerosomatic index; VW: villous width; WG: weight gain; WGR: weight gain ratio.

Table 5
Amino acid profile (% DM) of different insect meals used as fish meal replacement summarized from references.

Amino acid	<i>H. illucens</i>	<i>H. illucens</i>	<i>T. molitor</i>	<i>T. molitor</i>	<i>M. domestica</i>	<i>G. sigillatus</i>
Arginine	1.24	2.56	1.81	2.93	2.91	3.52
Histidine	1.07	1.50	1.77	1.71	1.63	1.35
Isoleucine	0.91	2.57	1.31	2.24	2.08	2.27
Leucine	1.86	4.12	2.96	3.98	3.41	4.25
Lysine	1.94	3.25	2.49	2.96	4.21	3.24
Methionine	0.47	0.91	0.57	0.68	1.40	0.97
Phenylalanine	2.16	2.03	3.07	1.78	3.81	1.90
Threonine	0.95	2.47	1.44	2.25	2.28	2.17
Tryptophan	-	-	-	-	0.71	-
Valine	1.42	3.53	2.32	3.08	2.80	3.16
Alanine	2.37	5.02	3.92	4.39	2.78	4.70
Aspartic acid	2.92	-	3.71	-	5.57	4.79
Glutamic acid	3.19	-	4.98	-	7.71	6.42
Glycine	1.84	2.98	2.87	-	2.33	2.68
Proline	1.58	3.81	3.04	4.05	2.27	2.92
Serine	1.43	2.73	2.49	2.74	2.18	2.87
Tyrosine	2.23	2.68	4.47	2.79	4.14	2.57
Cystine	0.13	-	0.24	0.21	0.53	0.53
Reference	Melenchón et al., 2022	Mastoraki et al., 2020	Melenchón et al., 2022	Mastoraki et al., 2020	Hashizume et al., 2019	Józefiak et al., 2019

without negative effects on growth performance and other physiological responses (Xiao et al., 2018; Wang et al., 2019; Abdel-Tawwab et al., 2020). When dried black soldier fly larvae meal replaced FM protein at percentages up to 20-64 % no negative effects were observed on fish growth, feed utilization, and survival rate, neither the hematological indices affected (Magalhães et al., 2017; Wang et al., 2019; Abdel-Tawwab et al., 2020; Adeoye et al., 2020). However, as reported with the use of some animal by-products, levels around 100 % negatively affected the growth performance, such as observed in catfish (Adeoye et al., 2020).

The potential role of the yellow mealworm (*T. molitor*) as an FM replacer is also increasingly being studied, due to its excellent nutritional value, accompanied by a short life cycle (Rema et al., 2019). Its inclusion at 25 % (corresponding to 33 % FM replacement) resulted in optimal WG, FCR, and PER in gilthead seabream (Piccolo et al., 2017), while in European seabass, anti-inflammatory activity was exerted (Henry et al., 2018) and in olive flounder immunostimulatory effect was observed in a range of inclusion from 13 to 52 % (Jeong et al., 2021). Moreover, in the study conducted by Su and colleagues (2017), the inclusion percentages of 9, 18, or 27 % of yellow mealworm meal in a yellow catfish diet induced an up-regulation of the major histocompatibility complex (MHC) II, IL-1, CypA (cyclophilin), IgM and HE (hepcidin) genes, thus demonstrating an immunostimulatory effect. Useful properties such as immunostimulant and against stress factors have been attributed to IMs, possibly due to components of insect exoskeletons (e. g., chitin and chitosan), which generally increase immunity by activating innate immune cells and inducing cytokines production through different cell surface receptor (Kamiliya and Khan, 2020). It was observed that the use of 30 % of larval frass rich in chitin for the presence of insect moulting, improves the innate immune response and the resistance of fish against *Flavobacterium columnare* and *Streptococcus iniae* infection (Yildirim-Aksoy et al., 2020). Other insect species approved by the European Commission for aquatic feeding (European Parliament, 2017) include *Musca domestica*, *Alphitobius diaperinus*, *Acheta domesticus*, *Gryllos sigillatus*, and *Gryllus assimilis*. The studies reporting the use of these insect species are listed in Table 6.

It is worth considering that different fish species have different levels of requirement for insects in their diet, which vary according to growth stages and farming systems; to commercialize IM in the future, these requirement levels must be known. One issue that certainly needs to be considered regarding the future perspectives of IM is consumer

acceptance, a necessary prerogative for successful IM supplementation into aquaculture. This acceptance could be accelerated by making information available for product awareness, starting for example with younger segments of the population, who are more willing to learn new concepts. The insect industry certainly needs to expand its production scale so it can compete on the price of other more common protein sources, as the production volume of SBM and FM is thousands of times greater.

4. Marine algae

4.1. Macroalgae

The Macroalgae, also called Seaweeds, are divided into three large groups based on their color. Green seaweeds, including more than 13,000 species, owe their color to the presence of chlorophyll a and b, which is used during the photosynthetic process. Red seaweeds (Rhodophyta) comprise 6100 species and their color is due to phycoerythrin and phycocyanin pigments; they contain a higher amount of proteins (up to 47 % of DM) compared to green and brown algae (Carpene et al., 2021). Among macroalgae species, red algae appear to be the most suitable source of animal feed due to their relatively high protein content and structurally diverse bioactive compounds with great pharmaceutical and biomedical potential (Younis et al., 2018). Brown seaweeds (*Ochrophyta*, *Phaeophyceae*) include 1800 species and the color is correlated with the content of carotenoid fucoxanthin. The protein content of the latter is lower than the other two classes, ranging between 5 and 15 % (Mohammed et al., 2021). From a regulatory point of view, within Europe, seaweeds that have been subjected exclusively to drying and crushing are referred to as “seaweed meal” (European Union Commission Regulation, 2022); otherwise, seaweeds subjected to other manufacturing processes are considered “novel feed ingredient”, regulated by European Regulation (EC) No. 767/2009.

Marine seaweeds represent a promising alternative to FM due to their low costs and relatively well-balanced essential AA composition (Table 7). Over 75 % of seaweed has higher proportions of total essential AAs than wheat flour, 50 % higher than soy flour, and also than rice and corn (Maehre et al., 2014). The inclusion of macroalgae could improve fish growth performance, or in any case not negatively affect them (Sotoudeh and Mardani, 2019; Zeynali et al., 2020). This was the case of a red sea bream (*Pagrosomus major*) fed with a 3 % diet inclusion of

Table 6

Insect-protein sources as a substitute for FM in the diet of different aquatic species.

Alternative protein source	Aquatic species	Inclusion levels	FM inclusion in the control diet	Time (weeks)	Effects	Reference
HIM	Siberian sturgeon (<i>A. baerii</i> Brandt)	185 g/kg (HIM25); 375 g/kg (HIM50); 750 g/kg (HIM100)	70 % DM	16	HIM100 was excluded from the study as fish refused the diet. Performance: ↓ feed consumption in HIM25 and HIM50; FBW in HIM50 than control; no difference in HSI and VSI; Digestibility: no difference in ADC of DM; ↓ ADC of CP in HIM25 and HIM50 than control.	Caimi et al., 2020
HIM; PBM	Crayfish (<i>C. cainii</i>)	39 % PBM; 32 % FM + 12 % HIM; 31 % PBM + 11 % HIM	41 % DM	8	Performance: no difference in WG and growth rate; ↑ haemolymph osmolality, LYS activity, total haemocyte counts, and protein and energy contents in the tail muscle (FM + HIM and PBM + HIM groups); Microbiota analysis: ↑ bacterial activity and gene function correlated to the biosynthesis of protein, energy and secondary metabolites (PBM + HIM group); <i>Proteobacteria</i> dominant in FM + HIM group, <i>Firmicutes</i> higher in PBM + HIM; Gene expression: Up-regulation of cytokine genes in the intestinal tissue (FM + HIM and PBM + HIM groups).	Foysal et al., 2019
CM	Nile Tilapia (<i>O. niloticus</i>)	20 % cricket meal (CM1); 30 % cricket meal (CM2)	-	6	Performance: ↓ FBW in CM1 than CM2; no difference in length; ↓ feed conversion factor in CM1 than CM2.	Cadena-Cadena et al., 2023
MD; SBM	Hybrid catfish (<i>C. gariepinus</i> ♀ x <i>H. longifilis</i> ♂)	300 g/kg SBM (SBM); 140 g/kg MD + 300 g/kg SBM (SBM+MD14); 210 g/kg MD + 300 g/kg SBM (SBM+MD21)	15 % DM	6	Performance: no difference in FCR, FI, PPV, LPV; ↑ FBW, WG, SGR, DGI of (SBM+MD21) than SBM and control (FM diet); no difference in HSI and VSI; Haematology parameters: no difference in Hb, RBCs, Hct; ↑ white blood cell and lymphocyte counts in (SBM+MD21); Immuno-physiological indicators: ↑ globulin value in (SBM+MD21); no difference in ALB, total IG, ALP, ALT; ↑ AST in (SBM+MD14) and (SBM+MD21); Antioxidant activity: ↑ SOD in (SBM+MD14); ↑ CAT in (SBM+MD21).	Fawole et al., 2023
MD	Nile Tilapia (<i>O. niloticus</i>)	110 g/kg (MD1); 220 g/kg (MD2); 330 g/kg (MD3); 430 g/kg (MD4)	360 g/kg	10	Performance: No difference in SR, WGR and SGR of MD1, MD2 and MD3 than the control group (FM diet); ↓ SR, WGR and SGR in MD4; no difference in HSI and VSI; ↑ FCR of MD4 than the control group; Innate immunity: no difference in serum LYS; ↓ macrophage phagocytic activity in MD2, MD3, MD4 than control.	Wang et al., 2017
HIM	Atlantic salmon (<i>S. salar</i>)	50 g/kg (HIM33); 100 g/kg (HIM66); 150 g/kg (HIM100)	10 % DM	16	Performance: no difference in FBW, WG, DGI, SGR, HSI, VSI, FI, FCR, CF, PPV and LPV; Digestibility: no difference in ADC of CP, CL, amino acids and fatty acids.	Belghit et al., 2019
HIM	European seabass (<i>D. labrax</i>)	65 g/kg (HIM6.5); 130 g/kg (HIM13); 195 g/kg (HIM19.5)	32.4 % DM	9	Performance: no difference in FBW and feed utilization; Hepatic antioxidant enzymes: SOD and CAT activity highest in control; no difference in GR and GPX.	Moutinho et al., 2021
TM	European sea bass (<i>D. labrax</i>)	25 % TM; 25 % TM + proteases (TM-Prot); 25 % TM + carbohydrases (TM-Carb)	70 % DM	6	Performance: no difference in FBW; HSI in all TM groups than control; Immunological analyses: ↓ activity of serum ceruloplasmin, myeloperoxidase and nitric oxide in TM diets than control; no difference in antibacterial activity of serum against <i>Micrococcus luteus</i> ; ↓ bacteriolytic activity against <i>E. coli</i> in TM-Carb than other groups; ↑ anti-protease activity in TM and TM-Carb than TM-Prot and control.	Henry et al., 2018
TM; HIM; MD	European sea bass (<i>D. labrax</i>)	19.5 % TM; 19.5 % HIM; 19.5 % MD	65 % DM	12	Performance: no difference in DFI; ↑ FBW in HIM than TM; no difference in WG and SGR; ↑ FCR in TM than MD and control; no difference in HSI, VSI and gut length; Plasma metabolites: no difference in AST and ALT; ↓ GLU in TM; ↑ CHO in HIM and control; Liver enzyme activity: no difference in AST and ALT; ↑ GDH in HIM than MD	Mastoraki et al., 2020
TM	Red seabream (<i>P. major</i>)	250 g/kg (25 % TM); 400 g/kg (40 % TM); 650 g/kg (65 % TM) 50 g/kg (5 % TM; challenge test for 8 weeks); 100 g/kg (10 % TM; challenge test for 8 weeks)	65 % DM	4	Performance: ↑ FBW in accordance with DMW inclusion; ↑ FI in accordance with DMW inclusion; Challenge test with pathogenic <i>Edwardsiella tarda</i> bacteria: ↑ in 10 % MW.	Ido et al., 2019
MD	Red seabream (<i>P. major</i>)	70 % undefatted MD larvae (-MD); 70 % defatted MD larvae (+MD)	70 % DM	4	Performance: no difference in BW and FI.	Hashizume et al., 2019
DTM	Pacific white shrimp	52 g/kg (DTM25); 103 g/kg (DTM50);	25 % DM	8	Performance: ↑ FBW in DTM50 and DTM75 than control; ↑ SGR in DTM50 and DTM100 than control; ↓ 24 % FCR in	Motte et al., 2019

(continued on next page)

Table 6 (continued)

Alternative protein source	Aquatic species	Inclusion levels	FM inclusion in the control diet	Time (weeks)	Effects	Reference
TM	<i>(Litopenaeus vannamei)</i> Meagre <i>(Argyrosomus regius)</i>	154 g/kg (DTM75); 205 g/kg (DTM100) 100 g/kg (TM10); 200 g/kg (TM20); 300 g/kg (TM30)	40 % DM	9	DTM50 than control; Immunity : ↓ PO activity in all groups after bacterial challenge with <i>Vibrio parahaemolyticus</i> . Performance : ↓ FBW, WG, FE, FI, PER with increasing TM inclusion; Digestibility : ADC of DM, CP and energy higher in control than TM diets; Hepatic amino acid catabolism enzymes : no difference in ALT, AST and GDH; Pancreatic digestive enzymes : ↓ Trypsin and lipase activities with increasing TM inclusion; no difference in α-amylase.	Coutinho et al., 2021
HIM; TM; GS	Rainbow trout <i>(O. mykiss)</i>	200 g/kg HIM; 200 g/kg TM; 200 g/kg GS	34.8 % DM	10	Performance : FBW and SGR lower in GS than TM and HIM; no difference in PER; Histology : ↓ villus height in TM and GS; ↓ mucosa thickness in GS; Microbial community : ↑ total number of bacteria in HIM, TM and GS than control (the highest value in TM); ↑ <i>Enterobacteriaceae</i> in TM than other groups; ↑ <i>Clostridium leptum</i> subgroup in TM and GS than HIM and control; ↑ <i>Clostridium coccoides</i> in HIM, TM and GS than control; ↑ <i>Lactobacillus</i> sp./ <i>Enterococcus</i> sp. in all treatments (the highest value in TM).	Józefiak et al., 2019
HIM	Rainbow trout <i>(O. mykiss)</i>	105 g/kg (HIM25); 210 g/kg (HIM50)	42 % DM	14	Performance : no difference in FBW, WG, SGR and FCR; Plasma metabolic parameters : no difference in CHO, TG, GLU, ALB and TP; Gene expression : no difference in <i>igf1</i> and <i>mstn1a</i> (fish growth) and <i>gr</i> and <i>hsp70</i> (stress response) genes; up-regulation of <i>hsp70</i> in HIM50; ↑ <i>il-10</i> , <i>tnf-α</i> , and <i>tlr-5</i> expression in intestine of HIM25 and HIM50; Histology : ↑ liver lipid accumulation in HIM50; no inflammation in intestine; significant shortening of the fold length of medium intestine in fish fed diets containing insects.	Cardinaletti et al., 2019
HIM	Rainbow trout <i>(O. mykiss)</i>	100 g/kg (HIM10); 200 g/kg (HIM20); 300 g/kg (HIM30)	60 % DM	12	Performance : no difference in WG and SGR; Digestibility : no difference in ADC of DM, CP and EE; Microbial community : ↓ <i>Proteobacteria</i> in HIM20 and HIM30 than control and HIM10; ↑ <i>Actinomycetaceae</i> , <i>Brevibacteriaceae</i> , <i>Corynebacteriaceae</i> , and <i>Microbacteriaceae</i> in all HIM diets than control; ↑ <i>Lactobacillales</i> in HIM diets than control; ↑ <i>Facklamia</i> , <i>Enterococcus</i> , <i>Lactobacillus</i> , and <i>Pediococcus</i> genera in HIM diets.	Terova et al., 2019
HIM	Rainbow trout <i>(O. mykiss)</i>	200 g/kg (HIM25); 400 g/kg (HIM50)	60 % DM	11	Performance : no difference in FBW, WG, SGR and PER; Digestibility : ↓ ADC of DM and CP in HIM50 than HIM25; Morphometric investigations : no difference.	Renna et al., 2017
TM	Rainbow trout <i>(O. mykiss)</i>	5 % (TM25); 10 % (TM50); 20 % (TM100)	20 % DM	22	Performance : no difference in FBW, WG, SGR, FCR, PER and FI; no difference in VSI; ↑ HSI in TM100 than control; Digestibility : ↓ ADC of CP with increasing TM level; no difference in ADC of DM, EE and GE; Hepatic enzyme activities : no difference in ALT, AST and GDH.	Chemello et al., 2020
TM; ZM	Sea trout <i>(Salmo trutta m. trutta)</i>	100 g/kg TM; 100 g/kg ZM;	25 % DM	8	Performance : no difference in FBW, BWG, SGR, FCR and PPV; ↓ PER in TM and ZM than control; ↑ HSI and VSI in ZM than TM and control; Blood serum immunology : ↑ AST in ZM; ↓ ALP in ZM than TM and control; ↓ TG in TM than ZM and control; ↑ ALB and CHO in TM and ZM than control; no difference in ALT, T-Pro, LYS, GLU, IgM; Gut histomorphology : no difference in villus height, villus width, and villus area of anterior part of the intestine. Microbial community : ↓ <i>Aeromonas</i> spp., <i>Enterococcus</i> spp. and <i>Carnobacterium</i> spp. in ZM; ↓ <i>Lactobacillus</i> in TM; no difference in <i>Bacillus</i> spp.	Mikołajczak et al., 2020
CM	African catfish <i>(C. gariepinus)</i>	75 g/kg (CM75); 150 g/kg (CM150); 225 g/kg (CM225); 300 g/kg (CM300)	300 g/kg DM	7	Performance : ↓ WG in CM75, CM150 and CM225; ↓ FCR in CM300.	Taufek et al., 2018

Abbreviations: ↑: improvement; ↓: decrease; ADC: apparent digestibility coefficient; ALB: albumine; ALP: alkaline phosphatase; ALT: alanine aminotransferase; AST: aspartate aminotransferase; BSF: black soldier fly meal; CAT: catalase; CF: condition factor; CHO: cholesterol; CL: crude lipid; CM: cricket meal; CP: crude protein; DFI: daily feed intake; DGI: daily growth index; DM: dry matter; DTM: defatted *Tenebrio molitor*; FBW: final body weight; FCR: feed conversion ratio; FE: feed efficiency; FI: feed intake; FM: fishmeal; GDH: glutamate dehydrogenase; GLU: glucose; GPx: glutathione peroxidase; GR: glutathione reductase; GS: *Gryllos* *sigillatus*; Hb: haemoglobin; Hct: haematocrit; HIM: *Hermetia illucens* meal; HSI: hepatosomatic index; IG: immunoglobulin; IGF: insulin like growth factor; IL-10: interleukin 10; LPV: lipid productive value; LYS: lysozyme; PER: protein efficiency ratio; PO: Phenoloxidase; PPV: protein productive value; SGR: specific growth rate; SOD: superoxide dismutase; SR: survival rate; TM: *Tenebrio molitor* meal; T-Pro: total serum protein; TG: triglyceride; VSI: viscerosomatic index; WG: weight gain; WGR: weight gain rate; ZM: *Zophobas morio* meal

Gracilaria lemaneiformis, which showed an enhancement of growth performance in terms of BWG and specific growth rate (Xuan et al., 2019). The replacement of a small amount (6 %) of dietary FM with *Padina australis* and *Sargassum ilicifolium* improved the growth performance and innate immune parameters in juvenile Asian sea bass

(*L. calcarifer*) (Morshedi et al., 2023), probably as a result of the improvement of intestinal morphology and the stimulation of digestive enzymes secretion. Good growth performance was also observed after the supplementation of 3 %, 6 %, and 9 % of *S. ilicifolium* in the Asian sea bass diet (Zeynali et al., 2020), and 6 % of the red seaweed *Gracilaria*

Table 7

Amino acid profile (% DM) of different macroalgae summarized from references.

Amino acid	<i>Gracilaria gracilis</i>	<i>Ulva rigida</i>	<i>Ascophyllum nodosum</i>	<i>Undaria pinnatifida</i>	<i>Sargassum muticum</i>
Arginine	1.3	1.51	0.10	0.53	0.48
Histidine	0.2	0.23	-	0.15	0.19
Isoleucine	2.3	0.94	0.02	0.38	0.41
Leucine	1.9	1.45	0.07	0.71	0.79
Lysine	1.6	1.24	1.85	0.57	0.49
Methionine	0.2	0.27	-	0.20	0.15
Phenylalanine	1.7	1.23	-	0.40	0.43
Threonine	1.7	1.10	2.24	0.44	0.40
Tryptophan	-	-	0.29	-	-
Valine	3.1	1.22	0.02	0.63	0.55
Alanine	1.9	1.78	1.67	5.29	0.80
Aspartic acid	2.6	2.87	0.88	1.24	0.99
Glutamic acid	2.4	2.32	1.20	1.71	1.17
Glycine	1.1	1.62	0.11	0.88	0.53
Proline	1.0	1.08	0.02	-	-
Serine	1.6	1.30	0.13	0.47	0.38
Tyrosine	1.3	0.86	0.04	0.24	0.25
Cystine	0.4	0.07	-	0.06	0.02
Reference	Batista et al., 2020	Ferreira et al., 2021	Vieira et al., 2018	Meng et al., 2022	Meng et al., 2022

pygmaea in rainbow trout (Sotoudeh and Mardani, 2019). The survival rate, growth performance, PER, chemical fillet composition (protein, lipid, and ash) (Fig. 4), and digestive enzymes (amylase and protease) were significantly increased in *Labeo rohita* fish fed with 100 g/kg of the red seaweed *Halymenia dilatata* (Manikandan et al., 2022). However, poor survival rate, FI, and growth indices were observed in fish fed a percentage over 10 % of this macroalga, associated with declines in AA levels due to the replacement of FM in the diet with excessive amounts of this alga (Manikandan et al., 2022). It is already known that feeding fish with excessive macroalgae interferes with nutrient utilization and adversely affects growth performance because they have a limited capacity to degrade non-starch polysaccharides (NSP), which are predominant in algae.

The supplementation of NSP-degrading enzymes in macroalgae-based diets (*Ulva prolifera*, *Gracilaria lemaneiformis*, or *Ulva pertusa*) has been demonstrated to improve the innate immunity of rabbitfish (*Siganus canaliculatus*), as the activities of serum lysozyme, SOD, and acid phosphatase were significantly higher in fish fed diets with the addition of macroalgae (Xie et al., 2019). Concerning the immune system of fish, in a study conducted by Nur and colleagues. (2020), the supplementation of the *H. musciformis* red seaweed at different FM replacement percentages (10, 20, and 30 %) in Tilapia fish diet demonstrated positive effects, with an improvement of Hb and hematocrit levels, thus indicating a better immune response. In particular, *Gracilaria* sp. by-products (ethanol extract and agar extract) were used as dietary supplements in gilthead seabream exposed to an acute crowding event with successful results in terms of oxidative stress mitigation and innate immunity improvement (Silva-Brito et al., 2020). Furthermore, *Gracilaria* by-products (2.5 % and 5 %) were able to reduce the stress levels of fish by lowering plasma cortisol, boosting the antioxidant response and finally decreasing GPx and GR activities in the liver.

Macroalgae are rich also in natural components with antimicrobial activity (e.g. polyphenols, terpenes, hydroquinones oligomeric phlorotannins, halogenated alkanes, and alkenes), as shown in seabream fish, where the supplementation with 5 % powder of *G. gracilis* resulted in the protection of the fish against *Photobacterium damsela* subsp. *piscicida* infection (Passos et al., 2021). Similarly, a 3 % of seaweed mixture (*U. lactuca*, *Jania rubens*, and *Pterocladia capillacea*) extract showed antimicrobial properties in striped catfish diet (*Pangasianodon hypophthalmus*), increasing the infection resistance against *Aeromonas hydrophila* (Abdelhamid et al., 2021).

4.2. Microalgae

Like macroalgae, microalgae could be useful as feed additives or replacements to FM, due to their capacity to synthesize nutrients and therefore produce an added high-value biomass, useful in aquaculture nutrition (Sagaram et al., 2021). As an interesting characteristic, microalgae can grow on some waste, including wastewater, converting organic components in eutrophic effluents into nutrients, including proteins, with well-balanced AA profiles (Table 8), lipids, and carbohydrates. In particular, they can provide a high percentage of proteins (30-40 %), with a high level of Met, synthesized, for example, in large amounts by the *Chlorella*, *Chlamydomonas*, *Porphyridium*, *Isochrysis*, and *Nannochloropsis* genera (Wan et al., 2019). In addition, their typical feature of lack of lignin improves the digestibility in fish (Niccolai et al., 2019).

In aquaculture, numerous studies were conducted on different fish species to test the effect of FM replacement with microalgae. The studies and the reviews published in the last 10 years agree on the evidence that using microalgae in fish diets supports health, survival rate, and growth performance. Particularly, they correlated with an improvement of FI, BW, FCR, and immune response, despite a percentage of inclusion too high could negatively affect these growth performance parameters (Jiang et al., 2019; Nagappan et al., 2021). Moreover, due to the nutritional value of microalgae, the fillet quality characteristics were improved (Nagappan et al., 2021; Ribeiro et al., 2017; Chen et al., 2019a) (Fig. 4). For example, the replacement of FM up to 15 % of CP with *Phaeodactylum tricornutum* and *Nannochloropsis salina* mixture, as well as mixtures of *N. salina* with *Amphora* sp. or *Cylindrothecaceae* sp. improved the hybrid striped bass performance, in particular the BW, FCR and protein retention efficiency (de Cruz et al., 2018). Effects were noted also in gilthead seabream and Nile Tilapia fed with microalga *Nannochloropsis gaditana* (2.5-5 % and 30 % of inclusion, respectively) (Ayala et al., 2020; Teuling et al., 2019) and in Nile Tilapia fed with *N. salina* meal (820 g/kg diet) (Gbadamosi and Lupatsch, 2018).

More recent studies report that diets supplemented with marine flagellated Chlorophyta *Tetraselmis suecica* provided to Pacific white shrimp (*Litopenaeus vannameis*) at a dose of 2.5, 5, and 7.5 g/kg showed an improvement in survival rate, BWG and FCR, with the up-regulation of the expression of antioxidant genes (SOD, GPx), lowest in the group fed the highest dose of microalgae (Sharawy et al., 2019). Contrarily, *T. suecica* (10 % of inclusion) did not influence growth performance, and nutrient retention in gilthead seabream juveniles (Pereira et al., 2020). However, at a dose of 15 %, as evidenced and common in many studies, was observed a decrease in the serum protein profile (TP, Alb, Glob, and their ratio) and enhancement in serum lysozyme activity, nitric oxide,

Table 8

Amino acid profile (% DM) of different microalgae summarized from references.

Amino acid	<i>N. oceanica</i>	<i>C. vulgaris</i>	<i>Spirulina</i> sp.	<i>S. platensis</i>	<i>Scenedesmus</i> sp.	<i>A. maxima</i>
Arginine	2.0	4.54	4.47	9.50	1.32	6.50
Histidine	0.6	1.04	-	2.20	0.52	1.80
Isoleucine	2.4	2.19	3.64	6.70	1.04	6.0
Leucine	3.1	4.25	6.17	9.80	2.12	8.0
Lysine	3.2	6.74	3.4	4.80	1.71	4.60
Methionine	-	1.00	1.71	2.50	0.52	1.40
Phenylalanine	1.8	2.67	3.33	5.30	1.40	4.90
Threonine	1.9	2.92	3.31	6.20	1.21	4.60
Tryptophan	-	-	0.85	0.30	-	1.40
Valine	5.1	3.21	4.21	7.10	1.50	6.50
Alanine	2.1	3.94	5.02	9.50	1.95	6.80
Aspartic acid	2.9	5.40	6.31	7.30	2.50	8.60
Glutamic acid	3.9	6.76	8.47	10.30	2.85	12.60
Glycine	1.7	3.87	3.43	5.70	1.66	4.80
Proline	1.7	2.81	2.53	4.20	1.42	3.90
Serine	1.3	2.72	-	5.10	1.10	4.20
Tyrosine	1.1	2.39	3.07	5.30	1.22	3.9
Cystine	-	0.2	0.64	0.90	-	0.40
Reference	Batista et al., 2020	Ferreira et al., 2021	Bashir et al., 2016	Koyande et al., 2019	Noreen et al., 2021	Koyande et al., 2019

and nitroblue tetrazolium levels (Abdelghany et al., 2020).

Among the best-known common microalgae, spirulina by-products (3 % of inclusion) and defatted *Haematococcus pluvialis* (12 % and 24 % of inclusion) administered to Nile Tilapia, showed an increase in BW, FCR, and protein efficiency at 12 % of inclusion but the 24 % of inclusion negatively affected the BW (Ju et al., 2017). Dietary supplementation with spirulina (*Arthrospira platensis*) powder in juvenile gibel carp improved the growth performance and survival rate of fish fed 3.38 and 6.76 g/100 g, and increased the plasma SOD and phagocyte activity of blood leukocytes (Cao et al., 2018).

5. Single-cell protein

Single-cell protein (SCP) refers to proteins extracted from pure or mixed cultures of microorganisms, such as microalgae, yeast, fungi, or bacteria, and can be used as a substitute for conventional protein sources intended for human and animal consumption (Pereira et al., 2022). Other names it can refer to are bioprotein, microbial protein, or biomass (Sharif et al., 2021). Their numerous advantages compared to traditional protein sources (e.g. high crude protein content (60–80 %), shorter production time, less use of land, ability to grow on a variety of substrates, absence of ANFs) have made SCP of particular interest in the aquaculture sector, especially as a valuable substitute for expensive protein sources such as FM and SBM (Ruiz et al., 2023). To reduce the production costs of SCP, several low-cost suitable substrates have been used so that the microorganisms can grow and produce tons of proteins. Such substrates include waste products from agriculture and industry (e.g. waste of fruit and vegetable processing, brewery wastewater) (Sharif et al., 2021). Although microalgae are part of the SCP group, for the purposes of this review they have been considered together with macroalgae in the previous paragraphs.

Over the past 10 years, the use of SCP has been examined in a panel of studies involving the main commercial aquatic species and showed its potential to replace FM and terrestrial plant proteins, especially in the case of yeast, or unicellular fungi (Glencross et al., 2020; Agboola et al., 2021). Compared to filamentous fungi, yeasts are more important in aquaculture research, so most of the studies in the literature focus on them. Yeast species normally used in aquaculture are considered the main protein-rich ingredient in aquatic feeds, due to their crude protein content of 38–52 % DM (Pereira et al., 2022). Yeasts in particular can convert low-value non-food biomass from the forestry and agricultural industries into high-value feed with less dependence on arable land, water, and changes in climate conditions (Lapeña et al., 2020). Hundreds of yeast species exist while only a few are used in aquafeeds, such as *Saccharomyces cerevisiae*, *Candida utilis*, *Kluyveromyces marxianus*,

Phaffia rhodozyma, and *Wickerhamomyces anomalus*, which act as sources of proteins, lipids, pigments and enzymes (Glencross et al., 2020).

The use of yeast as a source of dietary protein for farmed fish is not a new concept, as studies have been investigating this feasibility since the 1970s.

Recently, a study by Hansen et al. (2019) reported that Atlantic salmon parr fed diets containing *C. utilis* in combination with FM (20 %) or high levels of SMB (yeast percentages of 5, 10, 20 %) for 28 days had no negative effect on the intestinal structure, also showing high growth performance. Similarly, Nile tilapia fed diets containing different percentages (3, 5, 7 %) of *S. cerevisiae* for 84 days, showed a better growth performance and higher stress tolerance to hypoxia and disease resistance to *Aeromonas* compared to the control group proportionally to the inclusion level (Abass et al., 2018). *S. cerevisiae* supplemented with diet acts as an essential probiotic in Nile tilapia, as growth performance and feed utilization indices were increased significantly in the fish fed with the highest inclusion level (4 g/kg) compared to the control group (Islam et al., 2021). In addition, in the same group of fish an improvement in the absorptive surface of the intestine occurred (e.g. increase of length, width, and area of villi), consequently leading to improved absorption of essential nutrients and ultimately high growth performance of the fish (Islam et al., 2021). However, it should be considered that the digestibility of yeast is generally lower than that of FM and some plant proteins, so high yeast inclusions usually result in lower feed utilization and fish growth. This was the case of rainbow trout fed with 35.5 % of *Wickerhamomyces anomalus* + *S. cerevisiae*, which had a lower specific growth rate than fish fed FM (Vidakovic et al., 2020). The authors explained this result as a combined effect of lower FI and poorer protein quality. Similarly, a previous work conducted by Hauptman et al. (2014) reported that replacing more than 37.5 % (11.2 % dietary inclusion) of FM with dried grain distillers yeast in rainbow trout diets reduced growth performance, probably because of alterations in the quality of the pellet, which may affect the trout's ability to utilize nutrients.

Table 9 summarizes a selection of studies examining the effects of yeast and fungi on key aquaculture species.

Bacterial SCP generally carries the highest protein content (50–80 % DM) compared to the other SCP resources, and a high proportion of essential AAs, vitamins, and other valuable molecules. The most used bacterial species to produce SCP are *Methylobacterium extorquens*, *Methylococcus capsulatus*, *Rhodobacter sphaeroides*, *Affifella marina*, and *Corynebacterium ammoniagenes* (Pereira et al., 2022). The bacteria are very attractive as a source of SCP as they grow rapidly in different substrates as by-products from agroindustry and wastewater (Chumpol et al., 2018).

Studies addressing the application of bacterial SCP in aquaculture

Table 9

Fungal single-cell protein as a substitute for FM in the diet of different aquatic species.

Alternative protein source	Aquatic species	Inclusion levels	FM inclusion in the control diet	Time (weeks)	Effects	Reference
<i>Saccaromyces pombe</i>	Pacific white shrimp (<i>L. vannamei</i>)	10 g/kg (D2); 20 g/kg (D3); 40 g/kg (D4); 60 g/kg (D5)	60 g/kg	6	Performance: ↓ growth, feed utilization and PRE in D5; Proximate composition: no difference in protein, moisture, lipid, crude fiber and ash content	Qiu and Davis., 2017
<i>Rhodotorula mucilaginosa</i>	Nile tilapia (<i>Oreochromis niloticus</i>)	0.125 % (HY1) 0.25 % (HY2) 0.50 % (HY3) 1 % (HY4)	2 %	8	Performance: no difference in FBW, WG and survival rate; ↑ SGR and ↓ FCR in HY4 than control; ↓ VSI than control; Proximate composition: ↑ CP and ash in HY4 than control; no difference in moisture and lipid; Biochemical parameters: no difference in TP, ALB, CHO, TG, HDL and LDL; no difference in ALP among groups; Immunological and antioxidant parameters: ↑ LYS in HY2, HY3, HY4 than control; ↓ MPO in HY2, HY3, HY4 than control; ↑ TAC and SOD in HY2, HY3, HY4 than control; ↓ liver MDA in HY2, HY3, HY4 than control; no difference in liver TAC; Intestine histology: ↑ villi height in all groups than control; no difference in villi width; Bacteria challenge: ↑ survival rate against <i>Streptococcus iniae</i> in all groups than control	Chen et al., 2019b
<i>Aspergillus oryzae</i>	Nile tilapia (<i>O. niloticus</i>)	1 g/kg continuously (ASPC); 1 g/kg for 1 day and the next day with the basal diet (ASPF1); 1 g/kg for 1 day and the next two days with the basal diet (ASPF2)	80 g/kg	9	Performance: ↑ in WG, SGR, FER in ASPC than control; no difference in survival rate; Proximate composition: No difference for ash, moisture, lipid, CF, HSI and VSI; Digestive enzymes: ↑ lipase and protease in all groups than control; ↑ amylase in ASPC than control; Intestine histology: ↑ anterior, middle and posterior villi lengths than control; Blood markers: ↑ Hb in ASPC than control; ↑ Hct in ASPC and ASPF1 than control; ↑ RBC in ASPC and ASPF1 than control; ↑ Heterophils and lymphocyte in ASPC than control	Dawood et al., 2019
<i>Aspergillus niger</i>	Whiteleg shrimp (<i>Penaeus vannamei</i>)	125 g/kg (FR50) 150 g/kg (FR60) 175 g/kg (FR70) 200 g/kg (FR80) 225 g/kg (FR90)	250 g/kg	6	Performance: no difference in WG and SGR in FR50, FR60 and FR70 than control; ↓ WG and SGR in FR80 and FR90 than control; ↓ FCR in FR50, FR60 and FR70 than other groups; no difference in survival; Digestibility and digestive enzyme activity: ↑ ADC of DM in FR50; ↓ ADC of protein in FR80 and FR90; ↓ hepatopancreas protease with increase FM substitution; ↑ amylase in FR60 and FR70; Proximate composition: ↓ CL in control than other groups; no difference in moisture, CP, CF and ash	Dayal et al., 2020
<i>Candida utilis</i>	Shrimp (<i>L. vannamei</i>)	6.4 % (7T) 12.7 % (15T) 25.5 % (30T) 50.9 % (60T) 84.95 % (100T)	47.5 %	4	Performance: ↑ FBW in 15T than control; lowest FBW in 100T	Gamboa-Delgado et al., 2016
<i>C. utilis</i> (CU); <i>Saccharomyces cerevisiae</i> (SC); <i>Kluyveromyces marxianus</i> (KM)	Atlantic salmon (<i>Salmo salar</i> L.)	20 % (CU) 20 % (SC) 20 % (KM)	71 %	4	Performance: no difference in FBW; Intestine histopathology: examination of the distal intestine showed that all fish fed the SC diets developed characteristic signs of SBM induced enteropathy, while those fed the FM, CV or CU diets showed a healthy intestine.	Grammes et al., 2013
<i>S. cerevisiae</i> (SC) <i>Wickerhamomyces anomalus</i> (WA)	Rainbow trout (<i>Oncorhynchus mykiss</i>)	107 g/kg (SC20) 214 g/kg (SC40) 321 g/kg (SC60) 118 g/kg (WA20) 239 g/kg (WA40) 355 g/kg (WA60)	30 %	10	Performance: no difference in FCR; ↓ SGR in WA60 than control; WA40 diet reduced bacterial diversity, whereas the WA60 diet increased the abundance of the pathogenic yeast <i>Candida albicans</i> and reduced lactic acid bacteria in the gut	Huyben et al., 2017
<i>S. cerevisiae</i>	Rainbow trout (<i>Oncorhynchus mykiss</i>)	21.4 % (SC)	30 %	6	Performance: ↓ WG and SGR than control; ↑ FCR than control; Blood biochemistry and haematology: no difference; Intestinal histology: ↑ lamina propria inflammation than control; Intestinal gene expression: ↓ TNFα, IL1β, IL8 and CLD6	Huyben et al., 2019
Brewer's yeast (BY); Yeast hydrolysate (YH)	Pacific white shrimp (<i>L. vannamei</i>)	1 % YH 1 % BY	25 %	8	Performance: ↑ WGR and SGR in YH than control; lowest FCR in YH; Proximate composition: no difference in DM, CP, CL, and	Jin et al., 2018

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Table 9 (continued)

Alternative protein source	Aquatic species	Inclusion levels	FM inclusion in the control diet	Time (weeks)	Effects	Reference
<i>Cyberlindnera jadinii</i>	Atlantic salmon (<i>S. salar</i>)	10 % (FM10) 20 % (FM20)	676.8 g/kg	5	ash; Expression of inflammation-related genes: ↓ relative expression levels of <i>tnf-α</i> and <i>IL-1β</i> genes in YH; no difference in <i>alp</i> gene expression; highest expression of <i>tnf-α</i> and <i>IL-1β</i> genes in control; Expression of immune-related genes: highest expression of <i>proPO</i> in the control intestine; ↑ <i>dorsal</i> and <i>relish</i> expression in YH and BY than control; no difference in <i>lysozyme</i> expression; ↑ <i>penaeidin3a</i> and <i>crustin</i> expression in hepatopancreas of YH Performance: no difference in SGR; Gut microbiome: no difference in any of the alpha diversity measures tested across the groups	Leeper et al., 2022
<i>Yarrowia lipolytica</i>	Nile tilapia (<i>O. niloticus</i>)	3 % (YL3) 5 % (YL5) 7 % (YL7)	28.5 %	5	Performance: ↑ WG in all groups than control; ↑ total and standard length of fish in YL7 than other groups; Hematological parameters: no difference in RBC, Hb, Hct, MCH, MCHC, MCV; Immune response: no difference in total leukocyte and thrombocyte counts; ↓ lymphocytes number in all groups than control; ↑ plasma LYS in all groups than control; no difference in renal LYS; ↑ plasma nitrite/nitrate levels in YL3 and YL5 than control; ↑ renal myeloperoxidase in YL3	Neuls et al., 2021
Brewer's yeast	Giant freshwater prawn (<i>Macrobrachium rosenbergii</i>)	78 g/kg (Y20) 155 g/kg (Y40) 232 g/kg (Y60)	26 %	6	Performance: ↓ growth in Y60; ↑ FCR in Y60	Nguyen et al., 2019
Brewer's yeast	Thai Panga	90 g/kg (D30) 135 g/kg (D45) 180 g/kg (D60) 225 g/kg (D75)	30 %	36	Performance: highest FBW, WG, SGR in D45; ↓ growth performance in D60 and D75 than D45; no difference in FCR, FE, PER and HSI; Blood analyses: no difference in RBC, Hb, Hct, MCV, MCH, lymphocyte and platelet counts; no difference in CHO and GLU; ↑ ACH50, LYS activity and total immunoglobulin in all groups than the control; Proximate composition: no difference; ↑ redness and yellowness in the control	Pongpet et al., 2016
<i>Sporidiobolus pararoeseus</i>	Nile tilapia (<i>O. niloticus</i>)	5 g/kg (T2) 10 g/kg (T3) 20 g/kg (T4)	-	13	Performance: ↑ FBW, WG, ADG in T3 and T4 than control; no difference in survival rate; Blood analyses: no difference in TP, globulin, AST, ALT, CHO; ↑ ALB in T4; no difference in RBC, WBC, Hb, Hct, MCV, MCH, MCHC; Proximate composition: no difference in moisture, CP, CL, ash; Total carotenoid: ↑ in T4; Immunological parameters: ↑ LYS in T4; ↑ SOD in liver of T4 > T3 > T2; no difference in MDA values; Gene expression: ↑ <i>IL-1β</i> and <i>TNF-α</i> in spleen of T3 and T4; ↑ <i>IL-1β</i> in liver of T4; Challenge test with <i>Streptococcus agalactiae</i>: ↑ survival rate in T4	Van Doan et al., 2023
<i>C. utilis</i>	Atlantic salmon (<i>S. salar</i> L.)	25 %	15 %	8 Two periods: FW (0–28 days) and SW (28–56 days)	Performance: ↑ feed intake and higher growth rate than control; Histology and Morphometry: Immunohistochemistry: decreased length and number of CD3 labeled cells in the simple folds of fish fed control diet; Gene expression in DI and spleen: no difference in <i>IL-8</i> expression in DI; ↑ <i>Mhc1in</i> DI than control; ↓ <i>mhc1</i> in the SW period as compared to the FW period for both control and yeast; Protein levels of cytokines: ↓ <i>IFNγ</i> , <i>TNFα</i> , <i>IL-1β</i> , <i>IL-8</i> and in DI of fish fed yeast compared to control	Sahlmann et al., 2019
Intact <i>S. cerevisiae</i> (ISC); Extracted <i>S. cerevisiae</i> (ESC); <i>Rhizopus oryzae</i> (RHO); Blue mussels (<i>Mytilus edulis</i>) (MYE)	Arctic charr (<i>Salvelinus alpinus</i>)	289 g/kg (ISC); 172.6 g/kg (ESC); 260.1 g/kg (RHO); 220 g/kg (MYE)	46.8 %	14	Performance: ↓ FBW, SGR and WG in ESC and RHO than control; no difference in FCR among groups; no difference in HSI and VSI; Apparent digestibility: ↓ ADC for DM in RHO; ↑ ADC for CP in MYE and ESC than ISC and RHO	Vidakovic et al., 2016

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Table 9 (continued)

Alternative protein source	Aquatic species	Inclusion levels	FM inclusion in the control diet	Time (weeks)	Effects	Reference
Nucleotide (NT)-rich yeast	Pacific white shrimp (<i>L. vannamei</i>)	1 % (NT10) 3 % (NT30) 5 % (NT50)	17 %	8	Performance: ↑ WG, SGR and PER in NT50 than control; no difference in survival; Proximate composition: ↑ protein content in whole body of NT50 than control; no difference in DM, CL, ash of muscle; Serum biochemical parameters: ↑ TP and TG in NT50 than others; ↓ AST and ALT in NT50 than control; no difference in GLU and CHO; ↑ PO and LYS in NT50; Intestinal morphology: ↑ fold height and fold width in NT30; ↓ microvillus height in the control; Expression of immune-related genes: no difference in <i>acp</i> ; ↑ <i>alp</i> and <i>lzm</i> in NT30	Xiong et al., 2018
Yeast extract (YE)	Pacific white shrimp (<i>L. vannamei</i>)	4 % (D15) 8.5 % (D30) 13 % (D45) 18 % (D60) 25 % (D100)	25 %	6	Performance: No difference in WGR, SGR; ↑ FCR with increasing level of YE; Digestive enzymes in hepatopancreas: ↑ trypsinase with increasing level of YE; ↓ lipase activity than control; Proximate muscle composition: no difference	Zhao et al., 2017

Abbreviations: ↑: improvement; ↓: decrease; ACH50: Alternative complement activity; *acp*: acid phosphatase; ADC: apparent digestibility coefficient; ADG: average daily gain; ALB: albumine; ALP: alkaline phosphatase; *alp*: alkaline phosphatase; CHO: cholesterol; CL: crude lipid; CLD6: claudin-6; CORT: cortisol; CP: crude protein; DI: distal intestine; FBW: final body weight; FCR: feed conversion ratio; FDY: flash dried yeast; FE: feed efficiency; FER: feed efficiency ratio; FO: fish oil; FW: freshwater; GLU: glucose; Hb: haemoglobin; Hct: haematocrit; HDL: high density lipoprotein; HSI: hepatosomatic index; IL-1β: interleukin-1β; IL-8: interleukin-8; IFNγ: interferon-γ; LDL: low density lipoprotein; LYS: lysozyme; *lzm*: lysozyme; MCH: Mean corpuscular hemoglobin; MCHC: Mean Corpuscular hemoglobin concentration; MCV: Mean corpuscular volume; MDA: Malondialdehyde; mhc1: major histocompatibility complex 1; MPO: Myeloperoxidase; PER: protein efficiency ratio; PO: phenoloxidase; RBC: erythrocytes; SGR: specific growth rate; SOD: superoxide dismutase; SW: seawater; TAC: Total antioxidant capacity; TG: triglyceride; TGC: Thermal growth coefficient; TNFα: tumor necrosis factor α; TP: total protein; VSI: viscerosomatic index; WG: weight gain

nutrition are relatively few compared to those using yeasts, although their effectiveness has been repeatedly proven. The utilization of SCP produced from *M. extorquens* bacteria, known for the ability to consume methanol, was evaluated in rainbow trout to replace a portion of SBM (5–10 %) for 12 weeks. Results showed that an inclusion of up to 10 % improved fish survival, despite the slightly lower weight gain in fish fed the 10 % SCP diet, partly due to lower FI, resulting in a lower palatability of the diet (Hardy et al., 2018). Therefore, incorporating components that may increase palatability could further improve the results obtained. In white shrimp, the addition of *R. sphaeroides* and *A. marina* bacteria at different concentrations (1, 3, and 5 %) has been shown to provide some immunostimulant effect, promote growth, and increase survival of animals (Chumpol et al., 2018). Indeed, shrimps fed with the lowest concentration of bacteria (1 %) showed a higher growth performance and survival rate (85 %); shrimps fed the diet with 3 % bacterial SCP showed the highest total hemocyte count (THC) value, an indicator of health, while activities of phenoloxidase and SOD were significantly higher in all the groups compared to the control (Chumpol et al., 2018). Chen et al. (2020) tested the use of the protein of *Clostridium autoethanogenum* (CAP), a natural non-pathogenic strain used in the gas fermentation processes for biofuel production, as FM replacer in black sea bream diet for 70 days at six different inclusion percentages (4.85, 9.70, 14.55, 19.40, 38.80 and 58.20 %). Results showed that CAP could be added to the black sea bream diet to replace up to 58.20 % of FM protein without any negative effects on the growth performance of animals, and did not markedly affect the antioxidant capacity, measured as activity of hepatic SOD, CAT, and MDA (Chen et al., 2020). These results suggest that higher inclusion levels of CAP than these may also be tested in the same aquatic species. Another study demonstrated that CAP can be used in the largemouth bass diet at a level of inclusion up to 152 g/kg (150 g/kg FM replacing) without negative effects on growth, feed utilization, and intestinal histology (Yang et al., 2023). In another fish species, grass carp, the replacement of SBM with 50 g/kg CAP significantly improved the feed efficiency and WG, while higher CAP inclusion (100 g/kg) reduced the survival of fish and led to liver damage, which may be ascribed to the low arginine content in CAP (Wei et al., 2018). A

commercial SCP concentrate obtained from the bacteria *Corynebacterium ammoniagenes* (named PROTIDE) through a specific fermentation process, has been tested in whiteleg shrimp, demonstrating the suitability of this FM substitute at percentages higher than 10 and lower than 20 (Hamidoghli et al., 2019). Significant improvement in growth and feed utilization has been observed in barramundi fed diets supplemented with SCP derived from *Methylococcus capsulatus* at different percentages of inclusion (10, 20, and 30 %). This SCP proved to be highly palatable for barramundi, and healthy for the liver as indicated by HSI, triglyceride, and histopathology results (Woolley et al., 2023).

Despite the numerous studies mentioned above have demonstrated beneficial effects in several aquaculture species of fish and shrimp fed SCP-based diets (i.e. improvements in survival and growth performance, modulation of the intestinal microbiota, enhancement of innate immunity, and increased resistance to stress), there are still challenges to face in the increase of production, processing, and economics of SCP. Since the main industrial limitation of SCP is economic, it is necessary to develop strategies to reduce production costs and increase productivity, for example by developing more efficient fermentation systems.

6. New proposals for alternative protein sources to fishmeal

Like the animal by-products derived from poultry or livestock used in fish nutrition, crustacean processing discards contain valuable products including proteins, lipids, astaxanthin, organic acids, essential amino acids, chitin, and calcium (Prakash et al., 2012). For example, snow crab processing discards can potentially be recovered from processing industries, and converted into by-products such as crab meal with a higher content of CP and lipids (~51 % and ~16–25 %, respectively) or recovered for their high content of astaxanthin (33.8–39.6 µg/g) (Burke and Kerton, 2023). Other crustacean species have returned to the media spotlight for their national interest as invasive species for aquatic ecosystems. This is the case of the blue crabs *Callinectes sapidus* (Rathbun, 1896), *Portunus segnis* (Forskål, 1775), and *Procambarus clarkii* (Girard 1852), known as Louisiana crayfish.

The blue crabs, native to the American coast and Indo-Pacific Ocean,

respectively, have established themselves in the Mediterranean Sea (Mancinelli et al., 2021; Marchessaux et al., 2022; Shaiek et al., 2021) and neighboring waters, where they are currently considered an invasive alien species (Zenetos et al., 2005). Furthermore, the areas of expansion include also the Adriatic Sea and the Black Sea. Their biological characteristics such as early sexual maturity, rapid growth rates, opportunist diet, high reproductive rates, generalist habitat use, long-range larval dispersal, and effective physical and aggressive behavior (Castrìota et al., 2022; Mancinelli et al., 2017), make blue crab species efficiently invasive and with high potential of successful spread across sea areas. Additionally, their biological traits imply that they have the potential to impact benthic communities at multiple trophic levels. With similar biological characteristics to blue crabs, the Louisiana crayfish, which originated in North America, is an invasive exotic species of European importance (Black List), [European Union Commission Implementing Regulation \(2017\)](#), now widely spread in national and European internal sea waters. For the species included in this list, the same Regulation allows all eradication measures, including capture and subsequent disposal. However, today, the blue crabs are not yet included in this list.

Some studies have emphasized the high nutritional qualities of Mediterranean blue crab meat (Küçükgülmez and Çelik, 2008; Zotti et al., 2016) and Louisiana crayfish (Shahidi et al., 1998; Zaglöl and Eltadawy, 2009). It is evidenced that in *C. sapidus* blue crab, protein, fat, ash, and moisture of the breast, claw meat and hepatopancreas can be averaged of 19.05, 0.59, 2.10 and 76.85 g/100 g, respectively, with low differences of the protein contents in claw meat (19.55 g/100 g) than both breast meat and hepatopancreas (18.81 g/100 g) (Küçükgülmez et al., 2006). Similar results of the proximal compositions of *C. sapidus* blue crabs belonging to different sexes were observed by Tufan (2023). The average protein content in male and female blue crabs was 18.79 % and 19.11 %, respectively. The fat content in male crabs ranged from 0.46 to 0.69 %, whereas the amount in females ranged from 0.63 to 0.92 %, with a moisture and ash content in all of the body parts of both sexes varying between 78.62 and 76.73 % in males, and between 2.29 and 2.39 % in females, respectively.

Less data are available in the literature about the nutritional composition of Louisiana crayfish. The most recent data, relating to the whole product or meal, record a protein content varying between 40 and 75 % DM, a balanced AA profile, a high ash content, and a rather low lipid content in fat. Specifically, the chemical composition and nutritive value of crayfish showed mean values of TP, fat, ash, and cholesterol contents of 13.88 %, 1.76 %, 1.52 % and 13.575 mg/100 g respectively. Moreover, crayfish showed a higher content of PUFA (73.6 %) with 56.5 % and 15.08 % mono-ionic and poly-ionic fatty acids. Minerals concentration levels were 1.32 %, 506.33, and 415.63 µg/g for phosphorous, iron, and magnesium respectively (Zaglöl and Eltadawy, 2009). Overall, the crayfish meal is characterized by a high content of chitin (8 %) and carotenoids (119 mg/kg), of which approximately 90 % is made up of astaxanthin (Shahidi et al., 1998), which makes this ingredient very interesting for the diets of fish species of commercial interest in which coloring has added value, such as sea bream and rainbow trout. However, the typical color of blue crab claws is due to a natural pigment. These species are commonly consumed by human as food, but due to their nutritional characteristic, their processing waste could be used as valid feed ingredients or replacers to the FM. However, today its use is still little investigated and poorly considered. No less, it must be considered that, in addition to being intended for food production, these species are included in the list of [\(European Union Regulation, 2024\)](#) Reg. (EU) 1143/2014, which allows all eradication measures, including capture and subsequent disposal. Considering the emergency resulting from the high proliferation of invasive species such as the blue crab and the Louisiana crayfish, their usefulness as a new alternative source of animal proteins for aquaculture could be considered, after fishing and subsequent processing, safeguarding the feed safety aspects.

7. Conclusions

The most relevant result emerging from this study consists in highlighting that the alternative ingredients used up-to-date to fully or partially replace FM may affect several health parameters of aquatic species. In general, the inclusion levels of the different protein sources, plant- and animal-derived, ranged from 10 to 80 % and from 2 to 100 % respectively, in full or partial replacement of FM. The parameters positively affected are the growth performance, followed by the improvement of the immune status and antioxidant defense, and consequently a better general health, welfare, and fillet quality. Studies have shown a high variability of the inclusion levels, which could vary depending on the species and time of administration, as well as on the protein source production process. However, results clearly demonstrated that above a certain amount, the different protein sources can exert negative effects on fish growth performance, body composition, metabolic activities, and other biological parameters due to their ANFs (especially in the case of plant-protein sources). Although replacing FM with plant-based ingredients is considered environmentally sustainable, it should be considered that such a substitution would shift the demand for resources from oceans to land, potentially adding pressure to terrestrial food production systems, and impacting the environment, biodiversity, availability, and prices of crops.

New aquatic food resources to be commercially attractive should be available in large quantities, and competitively priced. At present, availability and low cost remain the major limitations for the use of several new alternatives in aquaculture feed.

Not all the new protein sources discussed in this review are available for the aquaculture feed industry and their direct use for aquatic feeding may be limited by several factors, including an unbalanced AA profile, a low protein quantity, or the presence of ANFs.

Plant-based by-products are commercially available, but their nutritional value is often too low to meet the nutritional requirements of some aquatic species, making necessary additional processing steps, which would also increase production costs.

Animal by-products are commercially available in large quantities and are commonly used as aquatic feed ingredients. In some European countries, consumer acceptance is limited, due to general misinformation, or for food safety reasons.

Furthermore, it should be considered that it is unlikely that a single protein source can satisfy the nutritional needs of a certain aquatic species, therefore, it is advisable to mix different protein sources to exploit the nutritional properties of each ingredient, observing synergistic or antagonistic effects. It follows that the future of aquatic feed formulations will probably be based on the blend of different protein sources, both of vegetable and animal origin. However, future research is necessary to determine which alternative proteins are the most suitable, in what proportions they should be included in diets, and how their nutritive value could increase, considering also their environmental impact.

The other main global issue that aquaculture is expected to face in the future is the progressive growth of the sector, which will have to satisfy the increasing demand for protein from an expanding global population. The aquaculture industry is large and complex and can include the possible farming of more than 650 species of fish, shellfish, aquatic plants, and algae grown in a variety of marine, brackish, and freshwater systems.

The global aquaculture policy priorities and outcomes do differ among countries (e.g. Europe, USA, Asia, etc.) for degree of success as measured by growth in fish supply and export, value chain development, environmental and spreading disease consequences, and distribution of benefits. The agro-climatic conditions, the economic policies, and the cultural orientation of a given country definitely affect the integration of aquaculture into food policies.

However, to consider these sources cost-effective and above all sustainable for their use in the future, other factors should be taken into

account, such as feed cost, costs of the farming system, and finally Life Cycle Assessment (LCA). Therefore, further efforts are still needed to find cost-effective ways to introduce alternative diets, ensuring both economic and environmental sustainability.

Ethical Statement

Any experimental invasive procedure in vivo was conducted for this study, and for these reasons, this research did not fall within the field of application of Directive 2010/63/EU on the protection of animals used for scientific purposes and therefore did not require specific authorization.

CRediT authorship contribution statement

Valentina Serra: Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Resources, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Grazia Pastorelli:** Writing – review & editing, Visualization, Supervision, Project administration, Investigation. **Doriana Eurosia Angela Tedesco:** Writing – review & editing, Visualization, Supervision, Investigation. **Lauretta Turin:** Conceptualization, Validation, Writing – review & editing. **Alessandro Guerrini:** Writing – review & editing, Writing – original draft, Resources, Methodology, Investigation, Formal analysis, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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