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REVIEW

REVIEWS IN Aquaculture

Future feed resources in sustainable salmonid production: A review

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Abstract

Aquaculture is one of the most resource-efficient and sustainable ways to produce animal protein. The Food and Agriculture Organization predicts that cultivated aquatic species will provide around 53% of the world's seafood supply by 2030. Further growth of intensive farmed aquatic species may be limited by a shortage of feed resources. The aquaculture sector therefore needs to intensify its search for alternative ingredients based on renewable natural resources. A significant increase in production will require an accelerated transition in technology and production systems, better use of natural available resources, development of high-quality alternative feed resources and exploitation of available space. The present review discusses the urgent need to identify appropriate alternative ingredients for a sustainable future salmonid production. We describe and evaluate the most promising marine ingredients, including low-trophic species (mesopelagic fish, zooplankton, polychaetes, macroalgae and crustaceans), novel microbial ingredients (bacteria, yeast and microalgae), insects (black soldier fly, yellow meal worm and crickets), animal by-products (poultry meal, meat and bone meal, blood meal and hydrolysed feather meal) and by-products from other commercial productions (trimmings and blood). Furthermore, we discuss the available volumes and need for new processing technologies and refining methods to ensure commercial production of nutritionally healthy ingredients. The essential production steps and considerations for future development of sustainable and safe seafood production are also discussed.

KEYWORDS
aquaculture, circular economy, emerging feed resource, ingredient, salmonid, seafood production

1 | INTRODUCTION

The growing demand for global food production requires the fundamental transformation of the aquaculture sector and better use of available resources and space.[1] Sustainable food production requires efficient use of readily available resources and a reduction in environmental impact and greenhouse gas emissions.[2–5] Land-based food production has the largest climatic impact, and therefore the food production sector cannot continue to grow unless more sustainable production methods are implemented. The greatest potential for increased food production lies in the oceans[6]; however, an increase in aquatic food production must come from farmed fish since 85% of the world's fish species are already maximally exploited.[7] Food and Agriculture Organization (FAO) have predicted that cultivated aquatic species will provide around 53% of the world's supply of seafood by 2030.[8] A projected increase of 26 million metric tons (MT) in global aquaculture production by 2030 will require an additional 40 million MT of feed.[9]

Salmonids are by far the most important domesticated species produced in the cold-water Nordic area and Northern countries, and the total production volume of salmonid accounts for <1.8% of the total global production share of farmed fish.[8] Norway and Chile are the world's leading salmonid producers, with respective shares of around 53% and 30% of the global salmon and rainbow trout production. Other major salmonid-producing countries include Scotland, Iceland, Faroe Islands and Canada. Salmon production increased from 151,000 MT in 1990 to >1 million MT in 2016.[10] Aquaculture is the fastest growing food production sector worldwide, and a future Norwegian scenario with an estimated production of 5 million MT of salmonids by 2050 is expected to require 6 million MT of feed.[11] Further growth in the aquaculture sector may be limited by a shortage of feed resources.[12] Thus, there is a need to develop alternative feed ingredients based on more efficient use of natural available resources from land and ocean, by exploitation of waste streams that is currently not utilised, and by improving processing technology to obtain safe and healthy aquafeed ingredients.

Worldwide, intensive research has been initiated to develop alternative sources of protein and essential *n*-3 long-chain polyunsaturated fatty acid (LC-PUFA) for use in aquaculture feeds due to stagnating and overexploited wild fish populations and the strong link with the destruction of rainforests for soy production.[9] Future feed resources are expected to include low-trophic species produced or cultivated in the ocean, such as mesopelagic fish and zooplankton (krill, calanus and amphipods), polychaetes, macroalgae and crustaceans. Ingredients can also be produced from land-based production, such as microbial ingredients (bacteria, yeast and microalgae), insects and animal by-products [ABPs; poultry meal, meat and bone meal, blood meal and hydrolysed feather meal (HFM)]. Resources derived from other commercial production, such as biodiesel, brewing and distillation industries, and by-products from the agriculture industry, can also be refined and used as feed ingredients.[13–15] New processing technologies and refining methods to produce ingredients of high nutritional quality with reduced levels of anti-nutritional factors (ANFs) and free from contaminants is essential for the development of sustainable and safe seafood production. The use of genetically modified organisms is controversial and not yet legal in some countries. However, this technique offers unique possibilities and should be explored in cross-sectorial platforms to address its use, benefits and consequences. As the competition for natural resources increases and technology advances, the production of some ingredients, such as microbial ingredients, is expected to gradually shift from being dependent on photosynthesis towards the use of a broader range of low-cost input factors, such as organic acids or CH_4, H_2 and CO_2 gas from industrial waste and other renewable energy sources. The predicted population growth and increase in demand for food requires legal authorities, producers, consumers and involved stakeholders to prepare for this in a future sustainable scenario.

Fish currently provide 16% of the animal protein consumed globally, and this proportion is expected to rise due to increased consumer demand for high-quality seafood. Novel ingredients may contribute to sustainable development in aquaculture without limiting the projected future growth.[9] However, it is essential to investigate all dimensions in sustainability and the trade-offs that novel ingredients may bring, including their impact on marine and terrestrial environments, biodiversity and ecosystem preservation, reduction in greenhouse gas emission and balance with social and economic outcomes. The goal should be aimed at validation through life cycle assessment methodology and land-use change (LUC) in carbon footprint climate impact.[16] The LUC approach suggests that feed ingredients should be ultimately produced without causing destruction of other ecosystems (e.g. deforestation) as well as close to where they are to be used to reduce emissions caused by long-distance transportation. Due to the complexities in production, regulatory and practical needs, improved collaboration across industrial actors, research fields, production levels and value chains are vital for the success of future sustainable aquaculture.

2 | HARVESTING AND CULTIVATION OF MARINE FEED RESOURCES

Current unexploited marine feed resources of significant biomass are found at lower trophic levels, mainly comprised by populations of animal plankton, mesopelagic fish and algae.[9] The harvesting of low-trophic species, such as Antarctic krill (*Euphausia superba*), Arctic krills (*Meganyctiphanes norvegica* and *Thysanoessa* sp.), copepods (*Calanus* sp. and others), amphipods (*Lysianassoide* sp. and others) constitute a huge biomass potential with an annual production of several hundred million tonnes (~600–700 million tonnes) of which only a fraction, mainly Antarctic krill, is currently harvested.[17] Fishing efforts from wild populations are typically managed well below their theoretical capacity due to environmental concerns,[18] but as the fisheries efforts are increasingly targeting the lower trophic levels,[19,20] there are increasing concerns about the effects on the ecosystem.[21] Intensification of harvesting and cultivation of marine species, alone or co-cultivated with other marine species in integrated multitrophic aquaculture (IMTA), will require use of large sea and land areas, both of which must be critically evaluated through appropriate impact studies.

2.1 | Antarctic and Arctic krill

Krill, the common name for the Euphausiids, is comprised of more than 80 shrimp-like marine crustacean families. Krill are found worldwide, and the species Antarctic krill (*Eup. superba*) has been exploited commercially as an ingredient in aquafeed. Antarctic krill is a free-swimming, low-trophic, plankton-feeding species that effectively brings nutrients into the food chain. Krill fishery is sustainable, monitored and regulated by independent international organisations, of which the Commission for the Conservation of Antarctic Marine Living Resources (CAMMLR) is the largest. Harvesting of krill is restricted to a specific region (Area 48, Antarctica), with an annual catch limit of 1% set by CAMMLR. The population of krill in Antarctica was estimated at 62.6 million MT in a biomass survey conducted by CCAMLR in 2019, and half of the annual quota of 620,000 MT is predominately caught by fisheries from Norway, China, South Korea and Chile. Krill are used to produce oil, meal and astaxanthin, a carotenoid with antioxidant properties that gives krill products their reddish colour, making it a high-value commodity.

The commercial potential of Antarctic krill in fish feed is largely associated with its nutrient content, large size (up to 6.5 cm and 2 g) and catch potential.[22] Fresh krill contains approximately 20% dry matter (DM).[23] The lipid concentration in whole krill ranges from 10%–40% DM, where fatty acid biomarkers show clear seasonal trends.[24] Krill oil is characterised by a high content of phospholipids, especially phosphatidylcholine, which comprise more than 30 g/100 g oil.[25] Krill oil contains high levels of the marine *n*-3 PUFAs, such as eicosapentaenoic acid (EPA) and docosahexaenoic acid (DHA), which are esterified to phosphatidylcholine.[26] The crude protein and ash concentrations in whole krill range from 7%–26% DM and 12%–17% DM, respectively.[23] Krill has a balanced amino acid profile and a high content of non-protein compounds, especially free amino acids (7%–8% DM).[27,28] The chitin content in krill is around 30 g kg^{-1} DM,[29] and astaxanthin levels in krill meal were shown to be 37 mg kg^{-1}, of which 95% were esters.[30]

Krill has been considered a palatable, high-quality dietary source of protein, energy and flesh-pigmenting carotenoids for salmon for several decades.[31,32] Studies have reported that consumption of krill improves growth in salmon,[33,34] although high dietary inclusion of whole krill, and hence high chitin levels, supresses growth.[33,35] The effect of dietary chitin on growth and nutrient digestibility has been reported in cod, salmon and halibut.[36] In a recent study in which krill meal was supplemented in plant-based/low fish meal diets to represent the current industrial practice, Mørkøre et al. reported improved gut health and meat quality of 4-kg Atlantic salmon (*Sal. salar* L.).[30] Microarray analysis revealed a krill-induced regulation of a number of genes, in particular cadherin, connexin and ladderlectin, which are involved in fat metabolism and deposition, cellular communication and pathogen recognition, respectively.

Krill meal is generally low in pollutants and the safety of krill powder has been mostly confirmed.[26] Although krill contains high levels of fluoride and copper, these did not appear to accumulate in the muscle tissue (fillets) of salmon. Increasing dietary krill inclusion levels leads to an increase in dietary fluoride levels, but a large fraction of this was excreted via the faeces without being assimilated, while assimilated fluoride was accumulated primarily in bones and scales.[23,31,37–40] Furthermore, it appears that fish reared in freshwater accumulated more fluoride in their bones, potentially due to a competing uptake from other ions in seawater.[40] Overall, no adverse effects on health or growth have been observed in salmon fed fluoride levels of 150–350 mg kg^{-1}.[23] The fluoride content in krill was mainly found in the exoskeleton and can be reduced if krill are deshelled before processing.[35,41] However, deshelling did not reduce the content of copper and cadmium, which are also high, although these may selectively accumulate in non-muscle tissue of salmon.[42] The European Commission Regulation 1881/2006 sets maximum levels for cadmium (Cd), a heavy metal that can be toxic to animals, in a range of foodstuffs and allows a limit up to 0.050 mg kg^{-1} of Cd in fish and crustacean meat products.[43]

Northern oceanic euphasiids are mainly comprised of the Northern krill, *Meg. norvegica*, with a co-occurrence of species from the genus *Thysanoessa* (*Thysanoessa inermis* and *Thysanoessa longicaudata*).[44] *Meg. norvegica* is thought to constitute the main biomass of krill in the Northern hemisphere, with a total biomass equivalent to that of Antarctic krill, ~380 million tons.[45] The nutritional profile of Northern krill resembles that of North Atlantic and Antarctic krill, although Northern krill shows distinctly different patterns of lipid deposition (total lipid of 10%–45% DM). The complex seasonal variations in the fatty acid content typically reflect the diet, and non-depot glycerophospholipids may constitute 3.5%–4.5% DM.[46] The Antarctic krill species have different strategies for lipid storage. Although *Eup. superba* primarily deposits triacylglycerols (TAG), the ice krill*Euphausia crystallorophias* and the krill*Thysanoessa macrura* mainly accumulate wax esters.[47] The digestibility of wax esters in feed for salmon can be lower than the digestibility of TAG.[17,48] The utilisation of low trophic species other than *Eup. superba* as future lipid resource for aquaculture therefore needs to be further studied. Consistent with Antarctic krill, Arctic krill species also contain astaxanthin esters as well as high levels of chitin, fluoride, copper and cadmium. Commercial harvesting of the Arctic krill species is not yet permitted, although some fishery trials have been initiated in Iceland and Norway to explore the commercial potential.

2.2 | Calanus

The marine copepod, *Calanus* sp., is an abundant marine zooplankton with a one-year life cycle and a biomass described as one of the largest renewable and harvestable resource in the Norwegian Sea.[49] Copepod species, including *Calanus finmarchicus*, *Calanus glacialis*, *Calanus hyperboreus* and *Calanus helgolandicus*, are present in the North Sea, Barents Sea and Northern Atlantic Ocean and *Calanus* sp. are also found in large quantities in the Labrador Sea between Canada and Greenland, along the east coast of the United States, and in the Irminger Sea between Iceland and Greenland.[50] Their abundance has recently been evaluated and fishing techniques to target *Cal. finmarchicus* have been developed. The annual production of

Calanus sp. shows seasonal variation, and the production estimates also show some variation based on the methodological approach for measuring of biomass. In the deeper Norwegian Sea basins, an annual production in the range of 193–290 million MT wet weight, with a standing biomass during the early summer (May–July) in between 29 and 45 million MT have been reported.[51,52] The recommended harvest from similar low trophic sources (e.g. Arctic krill) is 10%.[53] Commercial fishing of *Calanus* sp. has recently opened in Norway, with an established starting annual quota of 254,000 MT in 2019. Fisheries will be located far from the coast in areas with depths >1000 m, whereas up to 3000 MT can be fished closer to the coast in areas with depths <1000 m. The small and medium-size enterprise, Calanus AS, was awarded an additional research quota of 5000 MT, which can also be fished in shallow waters (https://www.fiskeridir.no).

Available *Cal. finmarchicus* stock levels have been evaluated by the Norwegian Institute of Marine Research (Bergen, Norway), and fishing technologies accordingly developed by performing of a trial fishery with a quota of 165,000 MT in 2016, A sustainable trawling method low in fishery by-catch using a specialised net and with up to 66% reduced fuel consumption compared with conventional fishing has been developed during the fishery trial period. *Cal. finmarchicus* contains 20%–23% DM, partitioned by 5% oil and 18% protein.[54] The *n*-3 LC-PUFAs in *Cal. finmarchicus* account for 20%–30% of the fatty acids in wax esters,[55] which is their main lipid storage component. Seawater acclimated Atlantic salmon can effectively utilise diets in which a major lipid component is derived from *Calanus*.[48] Bogevik have reported that Atlantic salmon hydrolyse fatty acids in wax esters slower than TAG, and feed and grow better on diets with a medium level of wax esters (30% of the lipid) compared to diets with a higher level of wax esters (50% of the lipid).[17] In Atlantic halibut, *Calanus* copepod oil was significantly less digestible than *Euphasia* krill oil and fish oil.[56] Despite some limitation due to high amounts of wax esters, the findings support the use of lipid from *Cal. finmarchicus* as an alternative or a supplement to fish oil and a provider of long-chain *n*-3 PUFA in diets for salmon. Human clinical studies have confirmed its safety and bioavailability.[57–59]

The carapace-rich side-stream from *Cal. finmarchicus* oil extraction may have potential use in various feed applications, and a liquid protein concentrate of *Cal. finmarchicus* is currently in use as feed stimulating ingredient in starter feeds for marine fish and prawn larvae (Skretting ARC). Commercial fishing has recently been opened, with 10 new licences awarded for *Cal. finmarchicus* fishing and processing from the Norwegian Institute of Marine Research (Bergen, Norway). The harvestable volume and number and variations of processing methods and yielding products is predicted to increase, thus opening the possibility for the sustainable use of *Cal. finmarchicus* both as a feed enhancer as well as a sustainable protein and lipid resource for aquaculture feeds.

2.3 | Mesopelagic fish

Mesopelagic fish are considered to have great potential as a source of marine protein and lipid for use as a sustainable feed resource in aquafeeds. Recent estimates suggest that there may be up to 10 billion MT of mesopelagic fish globally, which is 100 times more than the quantity of wild fish harvested each year by traditional fisheries.[60] Mesopelagic fish live at depths of 200–1000 m and include 30 identified families to date. They are mainly found in large quantities in the deep fjords and on the continental shelf in the Atlantic, Pacific and Indian Oceans. Gonostomatidae and Myctophidae are the dominant families worldwide. The largest biomass resources in the Northeast Atlantic include *Benthosema glaciale* (lanternfish, family Myctophidae) and *Maurolicus muelleri* (Mueller's pearlside, family Sternoptychidae). Deep-sea *Cyclothone* sp. (bristlemouths, Gonostomatidae family) are also abundant but may be of less commercial interest due to their small size and distribution in the lower mesopelagic layers.[60–62] No long-lasting economically sustainable fisheries on mesopelagic fish have been established, although a few promising stocks were explored during the early 1970s and 1980s. Mesopelagic fish originating from on-going fishery trials are currently used as raw material in conventional fish meal production on a basis of regulations provided along with mesopelagic grant permissions (The Norwegian Directorate of Fisheries, Norway). Due to high autolytic activity in mesopelagic raw material, methods for on-board processing of fish protein concentrate and/or hydrolysate to preserve the nutritional value and to improve growth performance and health responses in salmon,[63,64] are evaluated as commercial alternatives to conventional fish meal and fish oil processing.

Mesopelagic fish captured in the Northern Arabian waters consists mostly of Myctophidae sp., which are lean and bony fish that typically contain 65%–70% protein, 10%–16% lipid and 16% ash (dry weight), consistent with that reported for Pacific *Lampanyctus regalis*,[65] while also showing seasonal variation. Mesopelagic fish species are not only rich sources of high-quality proteins and lipids,[66,67] but also of minerals and bioactive compounds.[68] Fish harvested from low trophic levels typically contains mixed biomass of jellyfish, krill, shrimp, amphipods and mesopelagic fish and variations in the composition of the biomass are expected.[69]

The low content of persistent organic pollutants and other inorganic compounds reported suggests that oil from mesopelagic fish can be used as a sustainable and healthy alternative to conventional oils.[70] The content of LC-PUFAs, particularly DHA (22:6 *n*-3), is high and can help to meet the requirement for LC-PUFAs in salmon feed. A high content of monoene fatty acids, particularly oleic acid (18:1 *n*-9), has been reported in Myctophidae sp. catch during the early fishery trials in Norway in the 1990s. However, mesopelagic fish contain variable amounts of wax esters,[71,72] that may interfere with nutrient digestion in fish,[73,74] and/or cause problems with lipid extraction during processing. Potential anti-nutritional properties of mesopelagic wax esters have not yet been studied in salmonids. Limitations in the digestibility of *n*-3 LC-PUFAs present in the wax-rich oil from another low-trophic species, *Cal. finmarchicus*, was reported in Atlantic halibut,[56] while the wax esters were found to be well accepted in salmon when the Calanus oil was provided at a dietary level of 30% of the lipid.[17]

Commercial exploitation of mesopelagic fish is today limited by technical challenges related to capture, management and processing, and to a lack of knowledge of the resource potential for sustainable and bioeconomic harvesting. Fishing at great depths and far offshore is currently under strict regulation, and limited knowledge about the mesopelagic stock distribution and seasonal variation raises logistic problems that must be resolved to develop an ecosystem-friendly management of the mesopelagic fish resources. Mesopelagic research initiatives have been initiated in the Nordic and European regions to explore the potential for developing last-longing, sustainable and bioeconomic mesopelagic fishery.

2.4 | Marine macroalgae

The global production of aquatic plants (mainly marine macroalgae) reached 33.3 million MT (wet-weight basis) in 2018, of which >97% was from aquaculture (32.4 million MT).[10] The term macroalgae (or seaweed) refers to numerous species derived from three main classes: (1) brown macroalgae (*Phaeophyta*, >1500 species); (2) red macroalgae (*Rhodophyta*, around 7000 species); and (3) green macroalgae (*Chlorophyta*, 4500–8000 species).[75] The FAO reported >220 macroalgae species of commercial interest; however, <10% of these species are currently intensively cultivated,[76] such as *Saccharina japonica*, *Undaria pinnatifida* (brown kelps) and *Porphyra* spp. and *Gracilaria* spp. (red seaweeds). Macroalgae is currently used primarily for human consumption (both fresh and dried) or further processed to produce phycocolloids, such as alginates, agar and carrageenan.[77]

The chemical composition of macroalgae varies considerably, but is characterised by a large water content, typically around 90%, while the dry matter fraction consists of 3%–35% protein, 30%–60% carbohydrates, 2%–13% lipids and 10%–45% ash.[78–81] The protein content is typically lowest for brown seaweeds (3%–15% of DM), intermediate for green seaweeds (3%–35% of DM) and highest for red seaweeds (up to 47%).[79,81,82] Due to the high level of non-protein nitrogen (N) in macroalgae, a N-to-protein factor of approximately 5 has been suggested.[79,83] The proportion of essential amino acids (EAA) in macroalgae is similar or higher than fishmeal and soybean meal (mean = 45.7%, 43.4% and 46.0% EAA of total amino acids, respectively).[84] Compared to both fishmeal and soybean meal, the lysine proportion in macroalgae is usually lower, but most macroalgae species have a higher proportion of methionine than soybean meal.[81,84] Although red macroalgae in general have a higher protein level and protein quality than brown and green macroalgae, more variation exists between species within the taxonomic groups (brown, green and red macroalgae) than between the taxonomic groups.[84] Whole macroalgae inclusion at medium to high levels in aquafeed have often resulted in reduced growth performance of salmonids, but for omnivorous fish species such as tilapia, there are some promising results.[84]

In vitro digestibility tests using pepsin suggests that extracted seaweed proteins has a low digestibility, around 17%–57% relative to a casein standard.[85] However, in an in vitro protein digestibility assay of brown and red macroalgae with multienzyme hydrolysis, higher digestibility values were observed.[80] Interestingly, the same authors observed a strong inverse correlation between in vitro protein digestibility and the total phenolic content, indicating a necessity for refinement by removing both polysaccharides and phenols prior to aquafeed applications.[86] Fermentation has shown to increase in vitro digestibility threefold and appears to be a promising avenue to pursue.[82] Another approach is to extract proteins from macroalgae for use in aquaculture diets, but this will require major downstream processing.[87,88] Furthermore, to use macroalgae or hydrolysates thereof as a growth medium for yeast or insect production has been suggested.[89,90]

Few macroalgal species have been considered as potential aquafeed ingredients,[87] but there is an increasing interest in use of bioactive compounds with health benefits from seaweed in functional fish feed, such as laminarin, fucoidan, carrageenan, phenolics and carotenoids.[81,91,92]

2.5 | Cultivation of marine species

Fish farming releases significant amounts of solid and dissolved wastes, which may influence benthic and pelagic coastal ecosystems[93,94]; therefore, the rapid expansion of cage aquaculture has raised environmental concerns. IMTA is a promising ecological means to mitigate the effects of waste discharge from fish farms, while obtaining biomass production of co-cultured species.[95–98] In IMTA systems, fed aquatic species are combined with filter feeders and macroalgae to create a balanced system and circular use of nutrients. Several species have been studied and evaluated in a variety of systems. Macroalgae cultured close to salmon cages assimilate nutrients released from salmon farming and show higher growth rate.[94,99] Macroalgae (*S. latissima* and *Alaria esculenta*) are a superior source of minerals compared with terrestrial biomass, contain high-quality proteins and a wide range of bioactive components, which can have a range of different applications in fish feeds as discussed earlier. Filter feeders, such as blue mussels (*Mytilus edulis*) grown in proximity to salmon cages, can assimilate small organic particles of the salmon waste and produce a high growth rate in the spring.[100,101] Large particles originating from fish feed and faeces sink rapidly to the bottom,[102] where such wastes may be better utilised by deposit feeders, such as sea cucumbers.[103,104] This type of co-cultivation reduces the environmental impact and increases the resource efficiency and biomass production without the addition of energy in the form of feed.

Polychaetes (*Polychaete* sp.), amphipods (*Gammarus* sp.), tunicates (*Tunicata* sp.), clams and shells are all bottom feeders that prey on algae and other dead or wasted organic materials. The largest potential for these species as raw materials for aquaculture feeds lies in their selective cultivation or co-cultivation, rather than harvesting from wild populations, as the latter is unlikely to be financially or ecologically sustainable. Cultured polychaetes have the potential for diversification of aquaculture, either as the main crop species or produced in integrated systems with other species. The potential for cultivation of polychaetes was reviewed by Pombo et al.,[105] who highlighted existing species in production and potential new species. Although their focus was on aquaculture production of polychaetes for live bait, polychaetes may also play a role in aquaculture as wet feed or in the production of meal and oil. Most experimental work on polychaete culture in Northern Europe has focused on the common ragworm (*Hediste diversicolor*) as well as the king ragworm (*Alitta virens*) and lugworm (*Arenicola marina*). Rearing strategies for the commercialisation of polychaete production were pioneered by Olive,[106] highlighting the requirements of new production systems, environmental control and controlled breeding. *He. diversicolor* can be cultivated on a wide range of diets (faecal waste from fish, microalgae paste, fish flesh and formulated fish feeds) and exhibit high growth rates of 1.2%–6.5% per day depending on diet, temperature and life stage.[107,108] Polychaetes can be reared at high densities, depending on the species (and probably final size). *Perinereis helleri* has been successfully cultivated at 6000 individuals m^{-2},[109] minimising the physical footprint of production facilities. Polychaetes have been shown to have an excellent proximate composition, containing 55%–60% protein (N) and 12%–20% lipid on a DM basis,[108,110] with well-balanced amino acid, vitamin and mineral profiles, and high levels of PUFAs.[108,109] In addition to high growth rates, Brown et al. showed that the feed conversion of the sandworm *Nereis virens* was approximately 3,[110] meaning that 1 kg of polychaetes could be produced from 3 kg of aquaculture sludge from halibut production. The use of polychaete meal as an ingredient in formulated fish feed has not yet been tested.

Cultivated blue mussels (*My. edulis* L.) are also attractive as high-quality marine ingredients in aquaculture feed, with a worldwide production of 1.5–2 million MT, of which around one-third in Europe.[9] Blue mussels have a favourable amino acid composition,[111] and high levels of *n*-3 PUFAs and are reported to promote high growth rates in rainbow trout (*Oncorhynchus mykiss*).[112] They increase palatability of plant protein-based feed and can produce high growth rates in warm-water acclimated species.[113–115] However, high production and processing costs have made blue mussels less competitive for use in salmonid feed and cultivated mussels are currently mainly used for food purposes.

Tunicates have been found to be even more efficient than mussels in extracting organic resources due to their lower metabolic cost and high filtration capacity.[116] Despite a high protein content (47%–53% DM), cost-efficient production is difficult to obtain due to high water content (90%–95%) and need for dewatering. Industrial-scale cultivation methods for amphipods and tunicates have not yet been established and would require huge production volumes (>10–100,000 MT, w/w) to be relevant.

Harvesting and cultivation of new species at lower trophic levels are one of the designated focus areas in the circular bioeconomy. In IMTA systems, high-quality cultivated species can be produced for food purposes, while other species less suitable for food can be produced in large volumes and used in feed production or for other purposes, including remediation of environmental nutrient footprint of aquaculture actions.[117] The potential of IMTA can be further explored in a broader range of IMTA cultivated species. Moreover, the increased focus on the sustainable use of resources and the pressure to reduce the impact from traditional aquaculture implies that the search for new production systems and improved management practices and technology are expected to increase in the future.

3 | PLANT-BASED BY-PRODUCTS

Identifying different plant-based by-products for use as fish feed ingredients has received increasing attention in recent decades as the industry continues to search for alternative feed resources.[32,118] There are numerous examples of successfully applied plant-based diet ingredients, including soybean, corn, rapeseed, peanuts, cottonseed and sunflower.[119] In general, plant-based by-products have the potential as ingredients in diets for Atlantic salmon and will, thus, relieve pressure on the wild fish stock and have economic and ecological impact towards an efficient and optimal circular economy.[120,121] Use of plant by-products in diets for carnivore fish like salmon is, however, limited due to a high content of non-starch polysaccharides, a wide range of ANFs, poor palatability, and an unbalanced amino acid composition compared to the requirements.[122] Optimal feed formulation combined with new processing technology and use of exogenous enzymes as feed additives to improve nutrient digestibility of these by-products can offer a partial solution to this problem.[123]

3.1 | Brewers' spent grain

The beer and cider brewing industries generate large amounts of by-products for potential use as fish feed.[124,125] In addition, the recent rapid increase in the global number of small breweries has generated large quantities of brewing by-products that are available at low or no cost. Brewers' spent grain (BSG) is the most abundant brewing by-product and accounts for 70%–85% of the total by-products generated by the beer brewing process.[125,126] Spent grains account for approximately one-third of the original malt weight from beer production,[125,127] and ∼40 million MT of spent grain are produced globally every year.[126,128,129] BSG-based fish feeds have already been successfully evaluated and applied to some fish species, such as Nile tilapia, *Oreochromis niloticus*.[130] To our knowledge, there are currently no commercially applied methodologies using this material in salmonid diets, but there have been successful attempts to evaluate the suitability of this raw material in salmonid fish feeds.[131,132]

3.2 | Distiller's grains and distiller's dried grains with solubles

Distilled alcohols are produced by the distillation of liquid materials that have already experienced alcoholic yeast fermentation. Typical fermented materials include fruits, sugarcane, grains or vegetables, such as potatoes.[133] During the distillation process the liquid is purified and the diluting components (mostly water) are removed to increase the alcohol content to make it suitable for use in various industrial purposes or human consumption (liquors). More than

40 million MT of leftover materials, such as distiller's grains (DGs) or distiller's dried grains with solubles (DDGSs), are produced from the distillation process annually in the United States alone and have great potential as a source for fish feeds.[134] The rapid growth of the fuel ethanol industry has resulted in a phenomenal and continuing increase in the production of DGs.[133] Importantly, DDGSs also contain yeast, which is a valuable source of beta-glucans and nucleotides that may have enhancing effects on immune defence in fish. Efforts have already been made to use this source in aquaculture and the suitability of this material has been tested in both omnivorous species like tilapia and in salmonids like *On. mykiss* with positive results.[135–138] Diets containing up to 10% DDGSs have shown to support high growth performance in *On. mykiss*.[139] However, further studies are required to determine the optimal proportions of DGs and DDGSs for salmonid aquaculture.

3.3 | Rapeseed/canola cake

Rapeseed is a common oil crop grown in the Northern hemisphere. Its global production volume is 71 million MT, yielding 28 million MT oil and ~40 million MT of cake.[140] Around 28% of the global production volume is produced in Europe and 30% is produced in Canada, while the remaining 40% are produced worldwide in small quantities by other countries. Rapeseed has a crude protein content of 20%–23% on a DM basis and contains 43%–47% lipid and 12%–13% fibre.[141] Around 70%–98% of the oil content can be recovered, depending on whether oil extraction occurs by cold pressing or solvent extraction, resulting in rapeseed meal or press cake containing 35%–40% protein, which represents an attractive protein source in animal feed. The EAA composition in rapeseed is among the best of the plant-based protein sources but varies with according to source, pre-treatment and lipid extraction method.[141,142] Methionine and lysine comprise the first potential limiting EAAs that may restrict its inclusion level in fish feed.

The use of rapeseed cake as a raw material is limited by the high content of ANFs, including glucosinolates, tannins, phytic acid, sinapine, lignin, cellulose and hemicellulose.[142–144] These ANFs exert various adverse effects on growth performance and health of salmonids. ANFs found in plant-based protein sources and their effects on fish were reviewed two decades ago.[145] Enami reviewed the potential use of rapeseed and canola meal as a replacement for fish meal in aquaculture diets and concluded that up to 20% inclusion levels for salmonids was not a problem as long as fish meal was included for palatability.[146] The author highlighted the need for future studies directed towards the reduction or removal of ANFs in unrefined rapeseed meals.

The possibility of including unrefined rapeseed and canola cake or meal for aquaculture feeds has been studies since the 1970s, predominantly in species of tilapia,[147] catfish,[148] and salmonids.[149] In general, results show that moderate level of rapeseed meal of about 20% in diets for omnivorous species supported high growth performance, while higher inclusion level had adverse effect on performance. In salmonids, a meta-analysis on the use of plant ingredients showed that increasing the inclusion level of both canola meal and canola protein concentrate reduced growth rate in *On. mykiss*.[150] In general, processing to produce a protein concentrate provided better growth performance than using conventional meals. However, the meta-analysis showed that canola protein concentrates also had significant, negative effects on the growth performance of *On. mykiss*. The growth performance in *On. mykiss* was, however, not compromised by rapeseed diets based predominantly on protein concentrate or diets based on canola protein isolate.[149,151] Furthermore, Shafaeipour et al.[152] used a solvent-extracted canola meal to show that growth in *On. mykiss* fingerlings was not negatively affected by inclusion levels up to 300 g kg^{-1} (replacing ~25% of protein). Discrepancies among results regarding use of rapeseed and canola meal, or products thereof, in feed for salmonids remains unclear. This could be due to the differences in nutritional composition or quality of the ingredient, variable processing methods used to produce protein concentrates, as well as feeding regimen or fish genotype, age and environment as discussed by Collins et al.[150]

4 | MICROBIAL FEED RESOURCES

The increased demand for sustainable fish feed has led to an increased interest in alternative protein sources in aquafeeds. Microbial ingredients, such as fungi (yeasts), microalgae and bacteria have received increasing attention as alternatives. These ingredients have a low carbon footprint because they have a rapid growth rate, do not require any agricultural land, use little fresh water and can be produced from non-food biomass, CO_2 (microalgae) or natural gas (methanotroph bacteria). Overall, microbial ingredients can relieve the pressure on human food resources. Yeast and bacteria are examples of microbial ingredients that have been used in livestock feeds since the late 1940s.[153–155] In recent years, the increased demand for high-quality protein feedstuffs, advances in technology and reduced production costs have resulted in regained interest. Commercial production of microbial ingredients is under development and several start-up companies have been established, although current production volumes are not known.

4.1 | Yeast and filamentous fungi

Inactivated whole-yeast cells have recently received attention as potential sustainable ingredients in aquafeeds due to their ability to convert low-value non-food biomass from forestry and agricultural by-products or organic waste streams into high-value feed with limited dependence on arable land, water and changing climatic conditions.[15,156–161] Yeast can be produced from a wide range of feedstock. Use of first-generation feedstock has traditionally been the main carbon and energy sources, but concerns exist about the impact this may have on biodiversity, water and land use and competition with human food. Thus, there is an increasing interest in second-generation lignocellulosic biomass such as by-products from the agricultural and forestry sectors, as this represents an abundant, natural, renewable and cheap resource for biorefinery. Processing of lignocellulosic biomass from second-generation biomass such as spruce trees for yeast production requires four major steps as reviewed by Øverland and Skrede[15]: thermo-chemical processing pre-treatment that are adopted to the properties of the biomass, enzymatic hydrolyses, fermentation technology using special yeast strains to convert the sugars into microbial biomass and down-stream processing to produce a high-quality yeast-based protein source. The yeast cream is harvested, centrifuges and sprayed dried to a protein-rich powder. Processing of filamentous fungi is similar, but these fungi can grow on a wide range of substrates from different waste streams.[162]

The nutritional value of yeast depends on the species, fermentation conditions and downstream processing conditions after harvest.[158,163–166] The crude protein content of yeast ranges from 380 to 600 g kg^{-1} DM. Yeast also has a favourable amino acid composition compared with fish requirements but is often low in the sulphur-containing amino acids, methionine and cysteine.[161,167] In general, yeasts have a relatively low lipid content[168,169] and the fatty acid composition comprises mainly unsaturated fatty acids,[168,169] although oleaginous yeast, such as *Yarrowia lipolytica*, have a high lipid content with a high proportion of PUFAs.[170] The carbohydrates found in yeast mainly include polysaccharides, with low amounts of monosaccharides and oligosaccharides, except trehalose.[168] Microbial ingredients, such as yeast, have a high concentration of nucleic acids, which constitute 10%–15% in fast-growing yeast cells.[15,166,168,171] Nucleotides are considered as semi-essential nutrients and dietary nucleic acids may be partially salvaged and used by animals, thus positively influencing growth performance and N balance.[172,173] Fish species, such as salmonids, tolerate high levels of nucleic acids due to their efficient hepatic uricase activity.[171,174] In *Sal. salar*, the N retention increased after feeding *Cyberlinderna jadinii* (previously known as *Candida utilis*) containing 93 g kg^{-1} nucleic acids compared with a fish meal formulated diet,[169] which suggests that nucleic acids are directly incorporated into the body or spare non-EAA nitrogen via endogenous utilisation.

Most studies with fish have been conducted using *Saccharomyces cerevisiae* yeast. Positive effects of partially replacing protein from fish meal with *Sac. cerevisiae* yeast in salmonid diets have been reported.[165,175] However, high inclusion levels may reduce growth performance and nutrient utilisation in *On. mykiss* and *Sal. salar* due to low protein digestibility.[169,176] Other yeast species, such as *C. jandinii*, *Kluyveromyces marxianus* (previously known as *Kluyveromyces fragilis*), and *Wicherhamomyces anomalus*, are also of interest in aquafeeds due to their high nutritional value and ability to be produced from a wide range of substrates. Unlike *Sac. cerevisiae*, fewer studies have used *Cyb. jadinii*, *K. marxianus* and *W. anomalus* in salmonid diets. Previous studies have shown that *Cyb. jadinii* and *K. marxianus* yeast are promising protein sources for aquaculture that support high growth performance when replacing up to 40% of protein from fish meal in diets for *Sal. salar*[169] or when a mixture of *W. anomalus* and *S. cerevesiae* (70:30 mixture) replaced up to 40% of fish meal in diets for *On. mykiss*.[175,177]

Yeast contains a wide range of bioactive components, such as β-glucan, α-mannan, nucleic acids and antioxidants, with potential health beneficial effects. Several reviews have reported positive effects of low levels of yeast on growth performance, immune response and/or protection against bacterial infection and disease resistance.[178–181] Other studies have also reported positive health effects in the distal intestine in response to moderate levels of yeast in salmonid diets. The inclusion of 200 and 25–50 g kg^{-1} *Cyb. jadinii* yeast counteracted soybean meal-induced enteritis (SBMIE) in the distal intestine of *Sal. salar*.[182,183] Recently, Agboola et al. reported that inclusion of 50 g kg^{-1} of *W. anomalous* and *Cyb. jadinii* counteracted mild SBMIE in the distal intestine of *Sal. salar*.[161] *Cyb. jadinii*,[182] *W. anomalus* and *Cyb. jadinii*[161] have also been shown to modulate immune responses in *Sal. salar*. Furthermore, inclusion of *Sac. cerevisiae*, *C. jandinii* and *K. marxianus* to diets modulated intestinal microbiota in *Sal. salar*[182] and *On. mykiss*.[184]

The protein digestibility of yeast may be limited due to the content and characteristics of the cell wall, which limits access of digestive enzymes to the cellular content. The protein digestibility of yeasts in fish varies from 40% to 90%, depending on the species and strain of yeast, as well as the type of downstream processing used after fermentation.[169,171,185] Various chemical, enzyme, or mechanical methods have been applied to improve the digestibility of the yeast nutrients. These include mechanical rupturing of cell walls or enzymatic hydrolysis, enzymatic pre-treatment followed by high-pressure mechanical homogenisation, and processing by autolysis.[165,186] Processing via cell homogenisation and protein extraction[171] and autolysis[165] increase the protein digestibility of *Sac. cerevisiae* in *On. mykiss* and *Sal. salar*, respectively.

Filamentous fungus (*Paecilomyces variotii*) from spent sulphite liquor was used to produce Pekilo protein, a microbial ingredient that was used as an alternative protein source in farmed animals by the Finnish Pulp and Paper Research Institute in the 1970s. The protein content of this ingredient was 55%–63% and a digestibility of 87% was reported in monogastric animals. Carbohydrates mainly from the cell wall comprise around one-third of the total biomass, which is also rich in vitamins and minerals.[187] Pekilo protein is valuable for monogastric animals, such as pigs.[188,189] However, the nutritional value of Pekilo as a protein source for salmonids remains unknown.

4.2 | Bacterial meal

There has been interest in biotechnological production that uses waste or methanol for production of microbial ingredients for a long time. The first initiatives were developed in the 1970s and The Imperial Chemical Industries was the company first to initiate full-scale production and commercialisation of a microbial protein product called Pruteen, which was produced from methanol oxidation using *Methylophilus methylotrophus*.[152] Bacteria have the advantage of rapid growth on organic substrates, such as sugars and starch, as well as gaseous substrates, such as methane, hydrogen with CO_2 and/or CO_2 as a carbon source and syngas.[156,190,191] The key economic inputs for such products include the cost of goods and energy combined with high productivity and selling price.

Gas-based fermentation technology to produce methanotroph bacteria, such as *Methylococcus capsulatus*, from natural gas as the energy and carbon source is advancing.[192] Methane, which is the main component of natural gas, is found widely in nature and is an attractive substrate for bacterial protein production. Natural gas is abundant and cheap, making protein production from natural gas a realistic large-scale alternative. The naturally occurring methanotroph, *Me. capsulatus* (Bath), is highly efficient at converting methane to bacterial protein. Bacterial meal is produced from the fermentation of natural gas as a carbon and energy source using the methanotroph bacteria, *Me. capsulatus*, together with small amounts of the heterogenic bacteria, *Ralstonia* sp., *Brevibacillus agri* and *Aneurinibacillus* sp. Oxygen and ammonia are added to a continuous process together with a mineral solution. The bacterial biomass is continuously harvested, centrifuged and ultra-filtrated to remove excess water, followed by short exposure to high temperature to sterilise the product and finally sprayed dried to a powder with <10% water. Bacterial meal contains about 70% crude protein and 10% crude fat and resembles fish meal in macronutrient composition. The amino acid profile has some similarities to that of fish meal, although with a reduced content of lysine and methionine, and a higher tryptophan content. Bacterial meal grown on natural gas also contains around 8% RNA and 2% DNA, depending on the growth rate. Studies have examined the use of bacterial protein produced by natural gas fermentation as a protein source for several animal species, including pigs, chickens, *Sal. salar* and *On. mykiss*,[192] and have shown that bacterial meal is a high-quality protein source that supports high growth performance. Furthermore, no health problems have been reported when bacterial meal partially replaced conventional protein sources in nutritionally balanced diets.

Partial replacement of high-quality fish meal with increasing levels of bacterial meal (BioProtein) from 0% to 36% in salmon smolt diets in a 48 day's trial was found to improve growth performance and N retention of the fish.[193] In a long-term feeding trial with juvenile salmon in which up to 50% of the protein source was replaced with bacterial meal (BioProtein), the higher inclusion of bacterial meal (≥37%) resulted in reduced growth and survival rates.[194] Protein digestibility quantified in groups of 60 g salmon was moderately reduced with increasing bacterial meal inclusion, from 90% in the control diet to 84.2% at 50% inclusion.[194] It appears that juvenile salmon may be more sensitive to high bacterial meal inclusion than larger salmon smolt reared in sea water. An interesting candidate bacteria that show good potential as a protein source in diets for salmonids is *Methylobacterium extorquens. Met. extorquens* contain about 85.5% crude protein, and a high nitrogen and amino acid digestibility comparable to values for commercial fishmeal is demonstrated in Atlantic salmon.[195] Replacement of soybean protein by addition of 5% or 10% *Met. extorquens* in diets for rainbow trout increased the survival rate and did not negatively influence protein retention,[196] while a moderate level decrease in feed intake was reported.

Bacterial meal also contains a wide range of bioactive components, such as peptidoglycans, naturally occurring antioxidants and nucleic acids, which have a positive effect on gastrointestinal health in *Sal. salar*.[197–199] Gas-based fermentation technologies have been shown to be profitable due to lower natural gas prices, a higher demand for protein-rich feed resources and access to improved methods. This innovation has reached a new stage where international actors have taken the technology further towards commercialisation. Although the production volumes of bacterial meal are not known, several methanotroph-based bacterial meals are expected be available on the market soon, especially in areas of the world where there is access to cheap natural gas.

Although the use of natural gas offers new feed solutions, another option is to use bacteria such as acetogenic or aerobic carboxydotrophic bacteria in gas fermentation that can use different mixtures of gases, such as biogas, off-gases, H_2 and CO_2 as a substrate; however, this technology is still young.[200] Other examples include microbial ingredients produced using hydrogen-oxidising bacteria and electricity from solar panels to electrolyse water to produce hydrogen to feed the bacteria, CO_2 from the air, turning waste CO_2 into aquafeed and producing microbial ingredients (ProFloc) from bacteria grown on brewery wastewater and food waste streams or organic-rich process water.

Continued research and development into the production of microbial ingredients may make an important contribution to securing the sustainability of the agriculture and aquaculture industries. Advances in the microbial protein technology have been driven by large industrial actors in close collaboration with universities and research institutes. As the technology advances and the demand for such ingredients increases, industrial partners will play a larger role in advancing the technology. Large international industrial actors already have expertise in fermentation technology and can easily scale up to commercial production when the technology is shown to be profitable and demand from the feed market exists. As the technology advances, there is expected to be a shift in the production of microbial ingredients to become less dependent on photosynthesis and carbon as substrate and use of different gases, such as hydrogen and CO_2. This shift will be driven by an increased demand for natural resources due to competition for non-food uses, such as bioenergy, population growth, development of the bioeconomy and climate change.

4.3 | Microalgae

The term algae describe a group of taxonomically unrelated organisms that share numbers of traits (capability to photosynthesise as primary producers in aquatic ecosystems, etc.), and include cyanobacteria, eukaryotic microalgae and seaweeds.[201] In this section we will discuss microalgae, including cyanobacteria and Traustochytrids, encompassing genera such as *Schizochytrium* and *Traustochytrium*. Although debated to be algae, many of the commercial products based on species within this clade are marketed as microalgae products.[201,202] The estimated total microalgae production in Europe is 182 MT dry weight per year (excluding Traustochytrids) and 142 MT dry weight of the cyanobacterium, *Spirulina*.[203] The European microalgae sector comprises 74 microalgae producers and 222 *Spirulina* producers. The annual global production of microalgae biomass (excluding aquaculture hatcheries, which only produce for their own use) is estimated to be 25,000 MT dry weight, of which more than half is produced in China. The total market value is estimated to be €50 million and is expected to grow to €70 million by 2025.[204] Most of this biomass is used for food supplements, but other markets, such as animal and fish feed, are also targeted. Microalgae have been used in aquaculture applications for several decades, mainly for applications, such as in 'green water' hatcheries, as feed for mollusc larvae, echinoderms and crustaceans, as well as some fish larvae or their live prey (e.g., copepods and rotifers) or shellfish refinement.[205,206]

Microalgae contain a range of value-added components, such as proteins, lipids, carbohydrates, vitamins, antioxidants and trace elements, which are all interesting components in fish feed, either to replace conventional bulk ingredients, such as protein or lipids, or as a natural supplement for increased pigmentation or health benefits.[207,208] The composition and yield of microalgal biomass can differ for each species and can be, to a certain extent, controlled by the growth conditions or chemical composition of the cultivation medium.[209] Some species of microalgae have a high protein content (50%–65% of biomass), such as *Spirulina platensis*, *Arthrospira maxima* and some strains of *Chlorella* and *Scenedesmus*.[210] The amino acid composition of microalgae proteins is similar between species and comparable to conventional food and feed proteins, such as soybean protein.[211]

Microalgae can accumulate high quantities of *n*-3 PUFAs, which may account for 30%–50% of their total fatty acid content. For example, *Schizochytrium* sp, *Schizochytrium limacinum* and *Crypthecodinium cohnii* contain DHA and *Phaeodactylum tricornutum* and *Nannochloropsis* sp. contain EPA,[212–217] while *Pavlova* sp. can accumulate meaningful levels of both EPA and DHA.[218,219] Compared with heterotrophic species, the yield of *n*-3 PUFAs in photoautotrophic microalgae is low: *Ph. tricornutum* yields 5.5% EPA on a dry weight basis and *Nannochloropsis* sp. yields 4.8% EPA.[215,220,221] Efforts are ongoing to increase these levels significantly.[222–224] *Haematococcus pluvialis* algae meal is a good natural source of astaxanthin[225] and has been approved by the US Food and Drug Administration,[226] and by Japan and Canada for use in salmonid feed. *Duneliella salina* is another promising source of carotenoids as a dietary supplement for fish for both pigmentation purposes as well as health benefits.[227] Other health-promoting biomolecules from microalgae include beta 1,3-glucans, such as from *Chlorella* strains and *Euglena gracilis*, which can activate the immune system of various fish species.[228–230]

Different microalgae-based products, such as dried whole cells, ruptured cells, defatted cells (after lipid extraction) and extracts from various microalgal species, have been studied in feeding trials over the last decade, with different inclusion levels, nutritional profiles and feed processing treatments. The inclusion of various levels (1%–30%) of dried whole microalgae biomass in salmon feeding trials showed no adverse effects on growth performance, nutrient digestibility, or utilisation of the feed, although slightly impaired digestibility and improved biological activities were observed depending on size of the fish, species of algae, inclusion rate (*Arthrospira*, *Entomoneis* sp., *Nanofrustulum* sp., *Ph. tricornutum*, *Tetraselmis* sp.) and defatted biomass (*Desmodesmus* sp., *Nannochloropsis gaditana*, *Nannochloropsis oceanica*).,[207,231–236] Spray-dried *Schizochytrium* sp. has successfully been used to replace fish oil in *Sal. salar*, whereas long-term replacement of fish oil with whole-cell *Sc. limacinum* in salmon diets resulted in improved growth, anti-inflammatory effects and improved fillet pigmentation.[237,238] Dried whole cells of *Isochrysis* sp.[239] and *Schizochytrium* sp.[239,240] were also found to be good candidates for DHA supplementation in *On. mykiss* feed formulation. Replacing fish oil with *Schizochytrium* meal led to significant decreases in persistent organic pollutant levels in *Sal. salar*.[240,241] Furthermore, extracted microbial oil from a novel *Schizochytrium* sp. (T18) was found to be a sustainable high DHA source for Atlantic salmon feed performance.[242,243] On the other hand, Hart et al.[244] reported that whole cell biomass of *Schizochytrium* sp. had a high PUFA (98%) and protein digestibility in Atlantic salmon with no need for oil extraction or cell disruption. Tibbetts et al. observed that cell-rupture processing of whole cells of *Chlorella vulgaris* (inclusion levels up to 30%) greatly improved the apparent nutrient digestibility of juvenile *Sal. salar* diets.[245] A higher lipid and protein digestibility of feed containing pre-extruded microalgae (*N. oceanica*) compared with feed-added whole cells was reported in Atlantic salmon,[246] whereas cold-processed defatted microalgal biomass previously showed lower digestibility.[236] Tibbetts & Patelakis reported that adding up to 20% of intact-cell marine microalgae meal (*Pavlova* sp. 459) in diets for juvenile Atlantic salmon (*Sal. salar* L.) resulted in a high digestibility value of EAA and *n*-3 LC-PUFA of 92–99%.[247] The authors suggested that adding 20% of *Pavlova* sp. to salmon feed could satisfy *n*-3 LC PUFA requirements for Atlantic salmon.[247,248]

These studies show that some microalgae may be nutritionally beneficial and sustainable protein or lipid (*n*-3 PUFA) sources in salmon diets, as well as valuable source of pigments, antioxidants and vitamins. Optimal utilisation of the algae potential depends on appropriate pre-processing conditions of the algae biomass and feed processing conditions due to the cell wall structure that might limit the nutrient digestibility and, thus, the nutritional value. In addition to high nutritional value and palatability, the effects of microalgal inclusion on the physical pellet quality may also limit the possible inclusion levels of whole algae biomass. Gong et al. reported that increasing microalgae inclusion levels (*Scenedesmus* sp.) led to differences in feed colour (dark green), increased oily pellet surfaces but reduced fat leakage and produced harder pellets of shorter length.[249] Starch and non-starch polysaccharides and carbohydrate fractions in the algae biomass may affect the hardness of pellets.

5 | INSECTS

Entomophagy, the harvesting of insects for food, has been practiced for thousands of years in many cultures.[250] Rearing of insect's dates back thousands of years to when the cultivation of silkworms (*Bombyx mori*) for silk production began in China. The pupae by-product was fed to carp fish in ponds while the silk was harvested. The use of insects to convert food waste or cattle faeces and urine slurry into high-quality protein for animal feeds is relatively new, with the earliest studies published in the 1970s.[251,252] A milestone in European insect farming was the publication of the FAO manuscript 'Edible insects – future prospects for food and feed security'.[253] Interest in the transformation to a more circular food system increased at the time of publication and since then, research efforts have intensified and investments in the sector have led to more industrialised insect farming for food and feed purposes.[254,255] Pet food was the only feed market for insect protein in the European Union until July 2017,[256] when seven insect species including black soldier fly (*Hermetia illuscens*), common housefly (*Musca domestica*), yellow mealworm (*Tenebrio molitor*), lesser mealworm (*Alphitobius diaperinus*), house cricket (*Acheta domesticus*), banded cricket (*Gryllodes sigillatus*) and field cricket (*Gryllus assimilis*) were allowed for use in aquafeed. Soon afterwards, the aquaculture sector consumed >50% of the total European insect protein production, which was approximately 5000 MT in 2019.[257] Both insect production and the use of insect products in aquafeeds are predicted to rise, and more than €1 billion has been invested in insect companies to date.[257] However, despite substantial progress in research and the growth in insect production, current production is not sufficient for the extensive use of insects in aquafeed production. Many aspects, such as insect processing, automatisation of production and raw material processing need further attention.[257,258]

5.1 | Insect meals in feed

Despite the approval of seven insect species for use in aquatic feed in the European Union (EU); most insect meals used in salmon feed today come from black soldier fly and yellow mealworm larvae. Previously, there has been a debate on whether mealworms or fly larvae would be better suited for feed purposes. That discussion has since moved to the background due to the availability of better processing methods, resulting in improved insect meal quality for all species. Instead, the focus has moved towards other aspects of production, such as mass rearing and types of insect feed. Black soldier fly has received most attention in the past couple of years as a nutrient source for fish feed. Its larvae are omnivorous and can convert a wide range of wet organic waste streams; therefore, they can be produced anywhere there are large volumes of organic material available. They can feed on relatively low-quality, wet substrates, keeping production costs low. Black soldier fly larvae fed a good quality substrate, such as food waste, contain approximately 41% protein and 28% fat (dry weight basis).[259] The fatty acid composition of black soldier fly larvae differs to those of other insects, such as yellow mealworm and house crickets. The saturated medium-chain fatty acid, lauric acid (12:0), accounts for 21%–50% of the total fatty acid in black soldier fly larvae, making its fatty acid composition similar to that of coconut oil.[259,260] The nutritional properties and use of insect-based ingredients in aquafeed have been extensively reviewed previously.[261–265] Dietary inclusion of insect protein meal and/or insect oil in aquaculture diets without a negative effect on growth performance has been successfully demonstrated in salmonids,[266,267] and in some other fish species.[260,268–270] However, insect meals have also shown negative impacts on growth performances and feed utilisation in fish, mainly driven by changes in feed intake and nutrient digestibility.[271–273] A meta-analysis performed by Liland et al. concluded that diets containing 25%–30% insect protein do not reduce the performance of farmed fish, including *Sal. salar*.[265] However, comparing studies is not always straightforward as many of the aspects contributing to the quality of the ingredients (e.g., purity of raw material, chitin levels, processing and storage conditions) vary and are often not described. As more knowledge becomes available, the quality of ingredients can be improved, and older studies will no longer reflect new practices. A meta-analysis performed by Weththasinghe et al. concluded that the effect of insects on growth performance in salmonids depends on the reference diet used.[274] Adding black solider fly larvae meal in fishmeal-based diets reduced growth performance, while it improved growth performance when replacing plant ingredients.

5.2 | Protein content

Improved processing technologies have resulted in insect meals with a higher protein content and quality. Attention must be paid to calculating the protein content of insect meal. This is almost exclusively reported as crude protein calculated by using the standard N-to-protein factor of 6.25. However, insects contain high concentrations of non-protein N and the protein content is therefore often overestimated using this factor.[259,275] A N-to-protein conversion factor of 4.76 has been proposed for black soldier fly larvae, mealworm and lesser mealworm, whereas 4.53–4.80 has been proposed for house crickets.[267,275] Similar lower N-to-protein factors have also been recommended for microalgae and seaweeds ingredients.[276,277] Overestimation of the protein content may result in the formulation of underperforming diets, especially when higher inclusion levels are used.

5.3 | Chitin

The effects of chitin, the primary structural polysaccharide of the arthropod exoskeleton, are widely debated. The structural form of chitin reportedly inhibits nutrient absorption from the intestinal tract and therefore reduces protein and lipid bioavailability in mice and poultry,[278,279] whereas data in fish are inconclusive.[280] However, high dietary inclusion of whole krill, and hence high chitin levels, supresses growth in salmon.[33,35] Zarantoniello et al. recently reviewed the effects of chitin on microbiota.[281] Although chitin is generally considered not easily digestible by fish, chitinase activity has been found in the intestinal tract of many fish species. Atlantic cod have substantial chitinase activity in their stomach and pyloric caeca, while chitinase activity is not generally found in salmonids.[282,283] The in vivo digestibility of chitin by rainbow trout was shown to be less than 5%[284];

while it was reported to be more than 90% in Atlantic cod.[285] Chitin is one of the main growth substrates of lactic acid bacteria[286] and considered the 'core gut microbiota' in many marine and freshwater species.[287] These bacteria use chitin as a prebiotic and play a crucial role in making indigestible carbohydrates available, leading to better nutrient accessibility and utilisation for fish.[288] In addition, lactic acid bacteria contribute to the synthesis of vitamins and short-chain fatty acids, such as butyrate, which is an important anti-inflammatory molecule.[289,290] Whole insects contain 5%–25% chitin, and 35% of total chitin is found in the exoskeletons from black soldier fly larvae.[291] The chitin content of insect meal has been reported in only a few studies and can vary considerably.[262] The quantification of chitin remains challenging as this polymer is always associated with other compounds (protein, carbohydrates, lipids, or minerals) in insect meals. Furthermore, chitin is a hard, inelastic, *N*-acetylated amino polysaccharide, which is insoluble in water and most solvents, making its direct quantification challenging. However, new methods are under development that could be useful for future studies, such as the use of calcofluor staining.[292] It remains unclear whether chitin functions as an ANF or has prebiotic properties; however, it seems to have neither major negative nor positive effects in cultivated salmon.

Future challenges for insect farming for feed include competition for organic waste material with other new industries in the circular bioeconomy, which could drive the prices of insect feed materials up, as well as competition with the insect food market. This could mean that higher prices are paid for the insects used to produce the feed than for the feed itself. The establishment of regulations for insects to be used as food means that the market will start to consume more insect meal, which in turn will hamper the projected volume of growth for insect meal for feed.

6 | ANIMAL BY-PRODUCTS

The increased demand for food[8,293] and extensive use of small pelagic fish for direct consumption has led to increased use of marine animal by-products (ABPs) as important sources of oil and protein in feed for fish, livestock, pets and animals reared for fur. ABPs typically contain high levels of bones. The availability of nutrients (i.e. minerals and collagen rich proteins) in bones can be limited and inevitably lead to increased environmental load from fish feeds. The use of novel technology to increase bone nutrient utilisation and meet the requirements for sustainable aquaculture, is discussed below. Terrestrial ABPs are available in much larger quantities than marine by-products, but they are currently mainly used in salmon markets outside Europe.

6.1 | Marine ABPs

The global marine by-product volume from fishery is estimated to be around 5–6 million MT, as calculated from the total global capture of 96.4 million MT in 2018.[294] In European salmon-producing countries (mainly Norway, but also the United Kingdom, Ireland and Faroe Islands), the by-product volume accounts for about 1 million MT of fresh material,[9] equivalent to a bone raw material volume of 191,000 MT.

In fish bones, a high content of minerals, such as calcium and phosphorus, are present in hydroxyapatite [$Ca_{10}(PO_4)_6(OH)_2$], a poorly soluble, hence poorly available mineral complex.

About 71% of dietary phosphorus is released into the environment due to low phosphorus digestibility and excessive waste of salmon feed.[15] The very low digestibility of phosphorus in fish meal produced from blue whiting (*Micromesistius poutassou*) produced phosphorus deficiency signs in *Sal. salar*.[295] Phosphorus is an essential nutrient in aquaculture feeds as well as an important constituent in fertiliser for use in agriculture.[296,297] Although the extent of worldwide phosphates and its extractability and geographical concentration are debated, a European Sustainable Phosphorus Platform has been established to reduce the extensive waste of available phosphorus resources (https://www.phosphorousplatform.eu). Novel technology to recycle phosphorus and other minerals from fish bones have been developed and mineral ingredients produced from fish bones shown to be highly available in *Sal. salar*.[298–300] The fish bone ingredients have also shown added value properties for fish health and quality that make them attractive for use in aquaculture feed.[301] Novel methods to utilise the collagen rich protein in fish bones is currently explored to obtain a resource efficient production. Collagen products are of high market interest, but there are questions about economic feasibility of the new technology that must be resolved before the commercial potential can be fulfilled.

6.2 | Terrestrial ABPs

The global terrestrial meat production was estimated at 346 million MT of dressed carcasses in 2018, of which 250 million MT included poultry and pigs (https://ourworldindata.org/; accessed February 2020). Since the carcass usually constitutes around two-thirds of these animals,[302] of which some is bone, the potential amount of raw material for rendering is huge compared with the needs of salmon aquaculture. Nevertheless, only a limited amount of the global production of terrestrial ABPs is channelled into the logistic chains for use in salmon feed, and the exact volumes that are available and suited to aquaculture are unknown.

In the EU, ABPs are divided into three categories, of which only category three (carcasses or body parts passed fit for human consumption) can be used in feeds for production animals.[303] The rendering process provides two main fractions: animal fat and processed animal proteins.[304] ABPs available for fish feed can be further divided into poultry by-product meal, poultry fat, porcine meat and bone meal, blood meal (whole blood, haemoglobin meal and plasma) and HFM. Within these groups there are large variations in raw material composition, processing conditions and resulting nutritional quality.[34,137,305–314] In EU, by-products from poultry and pigs have been legally approved since June 2013, whereas by-products of ruminant origin are legally banned to eradicate transmissible spongiform encephalopathy.[315] Legislations lay down rules for minimum heat treatment of ABPs,[316] although it is known that heat treatment of raw materials may interfere with the digestibility of proteins and amino acids.[308,309,317–319] In Chile and Canada, ABPs, mainly of poultry origin, have been used as salmon feed ingredients for many years. In European salmon-producing countries (Norway, United Kingdom, Ireland and Faroe Islands), these products have not gained the same popularity since the ban was lifted in 2013. The reason for this is not clear but it may relate to a higher availability of fish meal and other protein sources and to a lower consumer acceptance.

Terrestrial oils, such as from poultry, are an interesting energy source in salmon diets due to their high availability and low price. They have shown to have no negative effects on growth performance in *On. mykiss* and *Sal. salar*.[320–322] The fatty acid composition of salmon fillets is strongly influenced by the dietary oil,[323,324] and a clear effect of fatty acid composition was found in fillet and whole body of salmon fed with poultry oil.[321,322,325] Reduced liver triacylglycerol levels were reported in salmon fed with diets added with poultry oil.[325] However, at the moment, the use of these terrestrial ingredients in salmon feed is limited.

7 | FUTURE PERSPECTIVES

Although novel ingredients are needed to bridge the gap in aquaculture feed resources, several challenges must be resolved to successfully implement these in the aquaculture industry. In addition to a high nutritional content, aspects related to technical quality, availability, cost and ecological sustainability need to be addressed. Many of the novel protein sources discussed in the present review are still not available for the aquaculture feed industry and their direct use for aquafeed is limited by several factors. Some ingredients have a low protein content and an unbalanced amino acids composition compared with the requirements of fish, and some may contain undesirable components that can reduce their nutritional value or cause nutrition-related health disorders, such as plant co-products (structural carbohydrate sources, such as lignin and celluloses), exoskeletons (chitin from insects and crustaceans) and microbial ingredients (cell wall material). Another limitation is the challenges associated with the physical feed quality. High physical pellet quality is essential to withstand logistic treatment (e.g., bulk transportation and pneumatic conveying) and extensive discharge of nutrients to the aqueous environment.[234,326–328]

Tacon[329] and Gatlin et al.[122] published detailed reviews on the ANFs present in plant-based feed (oilseeds and pulses), in which ANFs are divided into four categories: (1) protein-related (protease inhibitors, haemagglutinins, toxic amino acids and allergens); (2) glycosides (goitrogens, cyanogens, saponins and oestrogens); (3) phenols (gossypols and tannins) and (4) miscellaneous ANFs (phytic acid, anti-vitamins, anti-enzymes, mycotoxins and toxic fatty acids). ANFs present in both microbial-based[15,161] and insect-based[330] ingredients include structural carbohydrates in the cell wall fraction and chitin. A coordinated research effort is required to upgrade the nutritional value and to reduce undesirable components to increase their use in aquafeeds. Relevant technologies include solid-state or liquid-based fermentation, thermochemical, physical, or enzymatic treatment, selective crop breeding and application of genetic modification technology.

For novel aquafeed resources to be commercially interesting, they must be available in large quantities, have a predictable supply all year round and be competitively priced. Another aspect is high flexibility for their use in feed to ensure reduced risk and volatility for the aquaculture industry. At present, available volumes and economic feasibility remain a limitation for the use of several novel alternatives in aquaculture feeds. Several companies have invested in large-scale technological capacities to produce large volumes of *n*-3 PUFA alternatives, which are currently on the market. The capacity for insect production is increasing and several commercial-scale facilities are being built and ramping up their commercial volumes. Other resources, such as ABPs, are commercially available in large quantities and are commonly used as feed ingredients in salmon markets outside Europe. In European countries, such as Norway, the market acceptance of such ingredients is limited and influences the market adoption. Surveys conducted to investigate the rationale for consumer acceptance of ABPs and their use as ingredients highlights a lack of familiarity and an unclear perception of what ABPs are,[331] while the reason for rejecting by-products may be based on emotions and ideology, as well as questioning food safety and industry motivation.[332] Plant-based by-products are commercially available, but their nutritional value is often too low to meet the requirements for salmon feeds and would require additional processing steps, which would also increase the production cost.

8 | CONCLUSIONS

Changing climatic conditions and increasing competition for land, water and energy, as well as fully exploited capture fisheries, emphasise the urgent need for sustainable feed ingredients developed from underutilised natural resources. Microbial ingredients, such as bacteria and yeast, as well as insects, are receiving increasing attention as promising alternatives due to their ability to convert non-food organic waste streams from forestry, agriculture and food industries into high-quality nutrients without putting pressure on natural resources, independent of climate. To increase their share, these new ingredients must meet the requirements of being available in large quantities, having a predictable supply all year round and being competitively priced for functional use. The main strategies for improving the public acceptance for use of a broad range of ingredients should be to ensure the consumer of food safety and avoid associations with waste, as well as familiarising the public with the novel ingredients that are emerging in the circular economy. In the future, there will be more competition for natural resources driven by factors such as population growth, development of the bioeconomy and climate change. In this scenario, aquaculture will play an important role in meeting the global protein supply, developing novel technology and exploring the use of alternative sustainable feed ingredients.

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DATA AVAILABILITY STATEMENT

Data sharing not applicable to this article as no datasets were generated or analysed during the current study

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