CellPress REVIEWS

Review

Microalgal Aquafeeds As Part of a Circular Bioeconomy

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Photosynthetic microalgae are unicellular plants, many of which are rich in protein, lipids, and bioactives and form an important part of the base of the natural aquatic food chain. Population growth, demand for high-quality protein, and depletion of wild fishstocks are forecast to increase aquacultural fish demand by 37% between 2016 and 2030. This review highlights the role of microalgae and recent advances that can support a sustainable 'circular' aquaculture industry. Microalgae-based feed supplements and recombinant therapeutic production offer significant opportunities to improve animal health, disease resistance, and yields. Critically, microalgae in biofloc, 'green water', nutrient remediation, and integrated multitrophic aquaculture technologies offer innovative solutions for economic and environmentally sustainable development in line with key UN Sustainability Goals.

Highlights

Global population is forecast to increase rapidly by 2050, requiring a significant increase in food production, with special demand for high-quality protein.

The aquaculture industry is forecast to grow a further 37% between 2016 and 2030 and its heavy reliance on feeds produced from wild-caught fish is not sustainable.

There is a growing challenge of developing nutritious, sustainable aquafeeds from alternative sources while ensuring that farmed-fish supply meets consumption demands.

Development of the aquaculture industry is also constrained due to aquatic diseases caused by various pathogens.

Microalgae form the base of the aquatic food chain and contain essential amino acids, carbohydrates, lipids (including essential polyunsaturated fatty acids not produced by other organisms), and carotenoid pigments as well as antioxidants, immunostimulants, and antimicrobial compounds.

Increasing Demand for Aquaculture Feeds

Aquaculture (see Glossary) plays an increasingly important role in global food security, a critical challenge of the 21st century. The global population is forecast to increase from 7.6 to 9.8 billion by 2050[i], causing a projected food demand increase of 60–100% above 2005 levels [1,2]. In parallel, rising affluence is predicted to increase the demand for high-quality protein by 110% [2], emphasizing the need to establish sustainable[ii] high-protein food production networks. Currently, ~57% of global protein supply is from plant sources (almost exclusively terrestrial); the remaining 43% is from animal sources (red meat, poultry, seafood, dairy, eggs, and other products) [3]. Of the 1.7 billion tonnes year^{-1} of animal products produced globally in 2016[iii], wild-caught and farmed fish accounted for ~10% (171 million tonnes year^{-1}, US $143 billion) [4]. As wild-caught fish yields have plateaued over the past 20 years, fish demand has been met by an expanding aquaculture sector [4], which has increased from ~20 million tonnes (1950) to ~80 million tonnes (2016), at a growth rate of ~2.3 million tonnes year^{-1} (~6%)[iv].

Aquaculture's contribution to meeting future food demand will require more sustainable practices that support both aquatic and terrestrial ecosystems. A key problem to date has been the high use of wild-caught pelagic fish for the production of fishmeal and fish oil for formulated aquafeeds. This has put pressure on populations of low-trophic species that are keystones in aquatic food webs (e.g., anchovies, capelin, herring, mackerel, menhaden, sardines) and which wild fisheries depend on [5,6]. It also increases the potential spread of bacterial (e.g., *Vibrio cholerae* [7]) and viral (e.g., iridovirus [8]) diseases via raw fish distribution.

Fishmeal is a favored ingredient in fish nutrition as it is rich in protein, easily digestible, and palatable and provides a well-balanced source of essential amino acids, phospholipids, and omega-3 fatty acids such as eicosapentaenoic acid (EPA) and docosahexaenoic acid (DHA). Increasing use of alternative ingredients include those from animal, plant, algal, and microbial sources, each differing in their crude protein and fat content (Figure 1A,B, respectively).

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Crops such as soybean, canola, corn, lupin, wheat, and barley are widely used as protein substitutes (e.g., soy contributes ~60–70% protein in commercial aquafeeds for tilapia) [9] but are unable to provide sufficient levels of EPA/DHA [10], lysine, and methionine and can contain antinutritional compounds (e.g., saponins, tannins, soluble nonstarch polysaccharides) [11]. Therefore, only a certain proportion of the diet can be substituted before negative impacts on growth and health outweigh the benefits. As an example, Figure 1C compares the maximum recommended dietary substitution level of non-fishmeal feeds for tilapia, which is a prominent farmed fish. Furthermore, as the interlinkages between agriculture and aquaculture become stronger due to the production of crop-based feeds, the environmental impacts of aquaculture also expand (e.g., arable land use, freshwater use, agricultural runoff) [10].

A key challenge is to develop aquafeeds that can: (i) provide high nutritional quality; (ii) maintain sustainable food systems; and (iii) ensure that fish yields meet increasing demand [12].

Next-generation microalgae-based feeds offer promising food sources for sustainable aquaculture. Microalgae are the primary food source for zooplankton and lower-trophic fish that subsequently feed fish higher up the food chain and are a valuable source of key nutrients. Depending on the algal species and their growth conditions, they can contain up to 60% protein, 60% carbohydrates, or 70% oils [13] and produce valuable pigments, growth-promoting substances, and hormones as well as secondary metabolites that provide natural antioxidant, antimicrobial, anti-inflammatory, and immunostimulant benefits to aquatic animals [14,15]. Several species are also able to synthesize EPA, DHA, and pigments (e.g., carotenoids) *de novo.* Environmentally, microalgal production can support significant expansion of global photosynthetic primary production by farming on nonarable land or along coastal environments, reduce water demands and recycle nutrients by use of seawater and/or wastewater, and convert atmospheric CO_2 into nutrient-rich renewable feedstocks for high-quality feeds and animal health products. This provides the basis for a circular aquaculture industry as a part of a greater **circular bioeconomy** [16] and supports several **UN Sustainable Development goals**[ii], particularly #1-No Poverty, #2-Zero Hunger, #12-Responsible Production and Consumption, and #14-Life Below Water. Integrating algal production systems into aquaculture can create resource-efficient, ecofriendly value chains with a low carbon footprint [17] via coproduction of biobased and biodegradable products (i.e., a biorefinery approach) [16] while providing healthy diets and ecosystem services for the aquaculture industry and society more broadly [18].

This review highlights key advances in the development of microalga-based aquaculture feeds, essential to the development of a sustainable aquaculture industry.

Whole-Cell Feeds

Cultivated microalgae (e.g., *Chaetoceros calcitrans*, *Isochrysis galbana*, *Skeletonema costatum*, *Pavlova lutheri*) are used as **hatchery** and **nursery** feeds for shrimp, bivalve mollusks, and larval finfish and help to bring **broodstock** into spawning condition [19,20]. They are also fed to zooplankton, including rotifers, copepods, and brine shrimp (*Artemia* sp.), which in turn are fed to juvenile finfish and shellfish, including crustaceans (Table 1).

The demand for live algae has most commonly been met by on-farm production. However, such small and relatively low-productivity systems have resulted in high unit capital and operating costs and expensive microalgal feeds, estimated at 30–50% of the total fish production cost, depending on the type of algae and cultivations systems used [21–23].

Glossary

Animal therapeutics: therapeutic agents or compounds administered to animals to treat disease.
Aquaculture: also known as aquafarming, aquaculture is the farming of aquatic organisms (e.g., fish, crustaceans, molluscs, algae). Unlike commercial wild-catch fishing, aquaculture systems produce fish in more controlled environments.
Biofilter organisms: organisms that maintain water quality (i.e., oxygen, nitrogen, organic solids, and carbon dioxide concentration) in closed systems by removing pollutants from the environment.
Bioflocs: aggregates of microorganisms (e.g., algae, bacteria) and organic matter (e.g., fish waste, feed). They are nutritious, rich in protein, and foraged on by farmed species.
Broodstock: a population of mature organisms maintained for breeding purposes.
Circular bioeconomy: the intersection between the circular economy, which aims to reduce the inputs, wastes, energy, and emissions of a system, and the bioeconomy, which provides economic productivity through biotechnology and renewable biological sources. It promotes production from renewable biosources, extensive remanufacturing, reuse, and recycling of material and nutrient streams, cascading to maximize value and reduce waste, and resource-efficient and ecofriendly solutions.
Feed conversion ratio (FCR): the amount of fish produced from the amount of feed given (weight for weight).
Formulated feed: a quantified amount of feed ingredients that are combined to form a single uniform mixture (diet) that supplies all of an animal's nutrient requirements.
Green water aquaculture: a type of aquafarming in which ponds (usually freshwater) are inoculated by microalgal populations following fertilization (e.g., chemical, naturally nutrient-rich water). After inoculation, the ponds turn green, hence the name 'green water'. Green water systems can potentially be used to grow multiple freshwater fish species such as tilapia and carp. Additionally, they can be integrated with paddy fields, to coproduce rice as well.
Hatchery: a place where aquaculture eggs are hatched and the early-life-stage organisms are cared for.

Consequently, there is a growing trend to substitute live algae with more convenient, mass-produced off-the-shelf feeds including dried algae, concentrated algal pastes, **formulated feeds** (including microencapsulated feeds), bacteria, and yeasts [23–27]. Reported disadvantages of substitute hatchery feeds have included settling, aggregation, bacterial degradation, leaching of nutrients, low digestibility of the cell wall material, cell settling, and disintegration for dried algae [23,27]. Live microalgae are reported to be superior to other feed substitutes in terms of the enhanced growth and survival of **larvae** and **nauplii** of many species (e.g., bivalves) [23,28]. For example, the productivity of the Pacific geoduck clam (*Panopea generosa)* using spray-dried algae (*Schizochytrium* sp. and *Spirulina* sp.) was significantly reduced [28].

Recent improvements in feed technologies based on a better understanding of animal nutrition is enabling higher substitution of live algae without compromising animal growth and health [23]. For instance, a 75% substitution of dietary live algae with a formulated feed (MySpat^{TM}) was reported to achieve the same productivity in the green-lipped mussel (*Perna canaliculus*), reducing feed costs from US\$221 kg^{-1} to US\$138 kg^{-1} (conversion factor: US\$/NZ\$ = 0.68) [21].

High-quality concentrated algal pastes (e.g., *Isochrysis* sp., *Thalassiosira pseudonana*, *Tetraselmis* sp.) are promising replacements for live algal feeds. Similar growth rates have been reported for the use of commercial algal concentrates and live algae in the production of sandfish larvae (*Holothuria scabra*) [29] and winged pearl oysters (*Pteria penguin*) [30]. Typically, algal concentrates are produced by dewatering algae to a thick slurry (e.g., centrifugation, flocculation, filtration) and adding preservatives (e.g., antioxidants, food acids, cryoprotectants) [31]. These nonviable, intact, whole-cell, natural feed preparations are designed to retain nutrients and important characteristics (e.g., cell size, cell chemistry) beneficial for the feeding of early-life-cycle aquatic animals [19]. The cost of commercial concentrates ranges from US\$200 to US \$620 kg^{-1} [31][v], presumably due to the additional processing steps required and the market dominance of relatively few suppliers. Advanced large-scale microalgal production systems integrated with good cell harvesting, preservation, and storage and efficient distribution networks offer significant potential for cost reduction [22,31].

Formulated Feeds

Analysis of commercially produced ‘complete diets’, designed to supply all of the necessary ingredients for optimal fish growth, reported that these aquafeeds typically contain protein (18–50%), lipids (10–25%), carbohydrates (15–20%), ash (<8.5%), phosphorus (<1.5%), water (<10%), and vitamins and minerals (trace) [32]. Feed formulations are designed to optimize the **feed conversion ratio (FCR)**, which is important to boost fish production. This provides the added benefit of minimizing fish wastes and may be used as an effective tool to reduce life-cycle greenhouse-gas emissions of fish production [33].

Technically, aquafeeds within the above compositional ranges can be produced entirely from microalgae; however, other factors affecting the FCR to be considered include feed attractiveness (e.g., smell, taste), accessibility (e.g., cell/pellet size, buoyancy), and nutrient availability [34]. The high cell-wall recalcitrance of most microalgae is detrimental to digestibility and assimilation of intracellular nutrients, especially for carnivorous fish with a short digestion phase (e.g., salmon) [35]. Disruption of the cell wall of *Chlorella vulgaris* and *Nannochloropsis gaditana* has been reported to improve nutrient digestibility (especially for essential amino acids, carbohydrates, and starch) in Atlantic salmon (*Salmo salar* L.) [36] and protein and fat digestibility in Nile tilapia (*Oreochromis niloticus*) [37] but may cause the release of antinutritional compounds [38]. Cell-wall disruption can be achieved using mechanical, thermal, chemical, enzymatic, microwave, or ultrasound treatment [39], but the added benefits must be balanced with the costs.

Larvae: newly hatched fish. Larvae grow into fry and then fingerlings, which are both juvenile fish substages.
Nauplii: larvae of copepods are called nauplii, which is a plural form of nauplius.
Nursery: a place where juvenile fish are raised to contribute broodstock population.
UN Sustainable Development goals: 17 global goals were set by the UN in 2015 with the formal name ‘Transforming Our World: The 2030 Agenda for Sustainable Development’. These goals include Good Health and Well-Being, Clean Water and Sanitation, Affordable and Clean Energy, Decent Work and Economic Growth, Industry, Innovation and Infrastructure, Sustainable Cities and Communities, Responsible Consumption and Production, Climate Action, Life below Water, and Life on Land.

Currently, the relatively high cost of microalgae compared with common bulk meal ingredients (Figure 2) limits their use to high-value fish production [40]. Barone *et al.* estimated that algal meal prices of US$2.65 kg^{-1} and US$0.66 kg^{-1} were needed to replace fishmeal and soybean

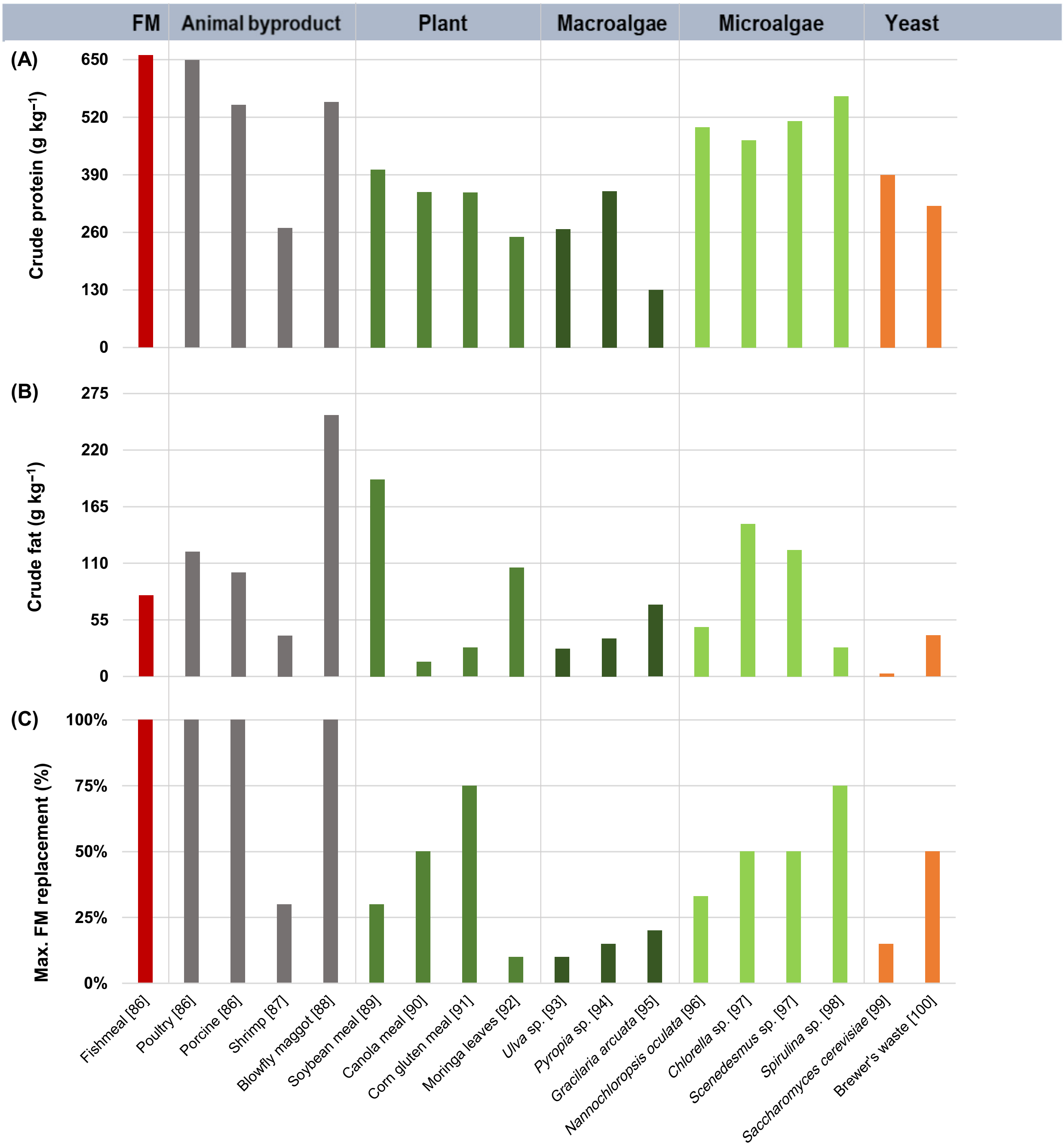

Figure 1. Comparison of Alternative Aquaculture Feeds with the Fish Meal (FM) Standard for (A) Protein and (B) Fat and (C) Maximum FM Replacement % in Tilapia (*Oreochromis* sp.) Diets [86–100].

Table 1. Major Microalgal Species and Their Applications for Aquaculture[a]

	Whole-cell feed						Formulated feed ingredient			Green pond farming	Animal health
	To aquatic animals			To zooplankton feed for finfish larvae and juvenile crustaceans			Algal meal	Omega-3	Pigments		
Microalgal species	Crustaceans (larvae)	Bivalves (all stages)	Urchins (larvae)	Rotifers (all stages)	Copepods (all stages)	*Artemia* (all stages)	Finfish, crustaceans (growout)		Salmonids, crustaceans	Freshwater fish, crustaceans, finfish larvae	All aquatic animals
Nannochloropsis sp.[Eu]	–	–	–	•	–	–	–	–	–	•	•
Chlorella sp.[Ch]	–	•	–	•	–	•	•	–	–	•	•
Pavlova lutheri[Ha]	–	•	–	•	–	•	•	–	–	–	–
Isochrysis sp.[Ha]	–	•	–	•	•	•	–	–	–	•	–
Tetraselmis sp.[Ch]	•	•	–	•	–	•	–	–	–	•	•
Chaetoceros sp.[Di]	•	•	–	–	–	•	–	–	–	•	–
Skeletonema sp.[Di]	•	•	–	–	–	–	–	–	–	–	–
Thalassiosira sp.[Di]	•	•	–	–	•	–	–	–	–	–	–
Haemotococcus pluvialis[Ch]	•	–	–	–	–	–	•	–	•	–	–
Nitzschia sp.[Di]	–	•	•	–	–	•	–	•	–	–	–
Navicula sp.[Di]	–	–	•	–	–	–	–	–	–	–	–
Amphora sp.[Di]	–	–	•	–	–	–	–	–	–	–	–
Phaeodactylum tricornutum[Di]	•	•	–	–	–	•	•	•	–	–	•
Spirulina and *Arthrospira* sp.[Cy]	•	•	–	•	–	•	•	–	–	–	•
Dunaliella sp.[Ch]	–	•	•	•	–	•	•	–	•	–	•
Schizochytrium limacinum[St]	–	–	–	•	–	•	•	•	–	–	–
Scenedesmus sp.[Ch]	–	–	–	–	–	–	•	–	–	–	–
Chlamydomonas sp.[Ch]	–	–	–	•	–	•	–	–	–	–	•
Euglena sp.[Ch]	–	–	–	–	–	–	–	–	–	–	•

Df, dinoflagellate; Eu, Eustigmataceae; Ch, chlorophyte; Ha, holotype; Di, diatom; Cy, cyanobacteria; St, stramenopile.
[a]Compiled from [22,27,101], except copepods [102], omega-3 [103], and animal health (see also 'Natural Immunostimulants and Growth Promoters' [57–68]).

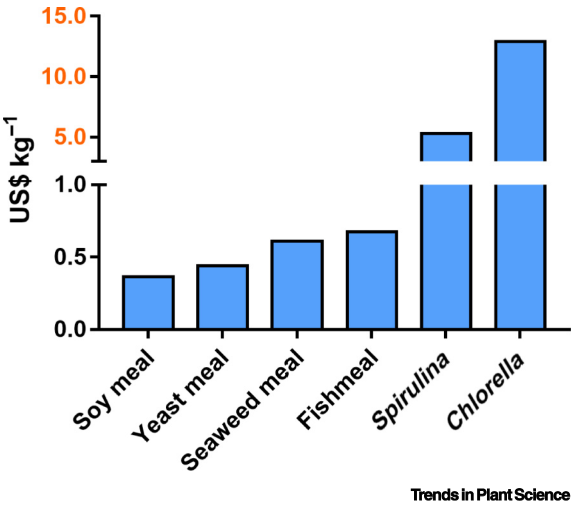

Figure 2. Price Comparison of Fishmeal Alternatives as Formulated-Feed Ingredients. All prices were obtained from various suppliers on [vii] as of September to December 2018.

meal, respectively, in the diets of tilapia (a relatively low-value fish) [41]. Given that algae are expensive to produce, their use as bulk ingredients for formulated feed production is likely to require improved production efficiency and further cost reduction through the use of biorefinery approaches [17]. However, the wide range of pigments, fatty acids, vitamins, minerals, and bioactives of microalgae make them excellent high-value nutrient additives and supplements to blend into a wide range of aquafeeds [35]. For instance, a 0.5–2.5% *Spirulina* sp. supplement improved growth rates, meat quality, coloration, and health, while reducing wastes [42].

Pigments

High-value carotenoids, such as β-carotene and astaxanthin, are widely used in aquaculture for their potent coloring and antioxidant properties, both of which can significantly improve the quality and value of the farmed fish (e.g., salmon, Asian tiger shrimp) [43]. The microalga *Haematococcus pluvialis* and *Dunaliella salina* synthesize large quantities of natural astaxanthin and β-carotene *de novo* (3–7% and 3–13% w/w, respectively) [44,45]. Estimated market sizes and product prices for common pigments produced by algae and their competitors are summarized in Table 2. Presently, cheaply synthesized pigments produced from petrochemicals account for almost all astaxanthin and β-carotene used as aquafeed additives [46].

Omega-3 Fatty Acids

Microalgae typically have a total lipid content ranging from 20% to 70% dry weight [13,47]; the long-chain polyunsaturated fatty acids DHA and EPA can range from 20% to 45% for high-yielding strains [48]. Their role in healthy aging, cardiovascular function, immune health, and the prevention of various chronic diseases [49] has led to a daily recommended intake of 500 mg of EPA/DHA for humans [50]. Fulfilling this global demand would require ~1.4 million tonnes[i] year^{-1}. Currently, production is ~15% of this quota, highlighting a key supply-and-demand constraint for human and aquacultural nutrition [50]. Moreover, increasing replacement of fishmeal and fish oil with plant-based ingredients is compromising the EPA/DHA levels and nutritional quality of farmed fish. For instance, it was found that farmed Scottish Atlantic salmon fed with an increasing level of plant-based feed over a 10-year period had reduced EPA/DHA levels in fish meat by 50% [51].

Microalgae (as feed and foods) present a potential solution to increased global omega-3 supply. However, a path to market-price reduction (Table 2) requires rapid scale up of advanced production technologies (ideally on nonarable land or in the oceans to maximize sustainability) and high-quality processing to preserve the biological activity (e.g., protection against oxidation) of EPA and DHA.

Animal Health and Growth

Aquatic diseases caused by viruses, bacteria, and other pathogens are a major concern for the aquaculture industry [52]. Industry-wide losses to aquatic diseases reportedly exceed US\$6 billion year^{-1} [53]. In shrimp farming, losses of over 40% of global production capacity (>US\$3 billion year^{-1}) can occur [52], mostly incurred by viral (~60%) and bacterial (~20) diseases [52]. Disease management has traditionally been based on the use of antibiotics or other chemotherapeutics [54], which are unable to treat viral infections and can increase pathogen resistance. Moreover, they can cause negative environmental impacts and are consequently subject to strict regulation [55].

To this end, the development of **animal therapeutics** – both natural and engineered – provides a significant high-value market opportunity for microalgae. Although not a panacea, certain microalgae have been reported to contain specific natural immunostimulants and antimicrobial compounds that increase resistance to aquatic pathogens [56].

Natural Immunostimulants and Growth Promoters

Numerous algal species (e.g., from the genera *Tetraselmis*, *Euglena*, *Chlorella*, and *Spirulina*) and algal compounds, such as sterols and unsaturated fatty acids, are reported to possess antibacterial activity *in vivo* and *in vitro* against several *Vibrio* species and other fish and shrimp pathogens, leading to improved survival rates [57–60]. Dietary *Chlorella* or *Euglena* supplementation was also shown to improve the growth performance, as well as the adaptive and innate immune response, of Gibel carp (*Carassius auratus gibelio*), the freshwater fish rohu (*Labeo rohita*), and the giant freshwater prawn (*Macrobrachium rosenbergii*) by increasing their resistance to the disease-causing bacterium *Aeromonas hydrophila* [61,62]. *Nannochloropsis*, *Phaeodactylum*, and *Tetraselmis* microalgal supplementation reportedly enhance defense activity in gilthead seabream (*Sparus aurata*) [63]. *Spirulina* has been reported to increase immune responses in carp (*Cyprinus carpio*) against *Aeromonas hydrophila*, in Nile tilapia (*O. niloticus*) against *Pseudomonas fluorescence*, and in great sturgeon (*Huso huso*) against *Streptococcus iniae* and other bacteria [64–66]. In addition, dietary application of *Dunaliella salina* to Asian tiger shrimp (*Penaeus monodon*) improved their reported survival rate when challenged with white spot syndrome virus (WSSV) [67], making *D. salina* an interesting candidate for recombinant production of disease-specific immunostimulants. The benefits of these different microalgae suggest that there may be some broad-based rather than highly specific advantages to fish health, such as improved microbiome composition [68].

Recombinant Therapeutics

In recent years, microalgae have been genetically engineered to produce a range recombinant bioactives, such as immune stimulators, vaccines, growth promoters, and antimicrobial agents for humans and animals [56].

Currently, recombinant products require extraction and purification for therapeutic use. Changes in the regulatory approval and market acceptance, however, of orally delivered alga-based therapeutics (in inactivated or live cells) could provide a much-needed low-cost disease management approach for the aquaculture industry. Furthermore, they could reduce the need for intraparenteral/intramuscular injection of vaccines, which are labor intensive, unable to be administered in high throughput to small/juvenile fish or crustaceans, and cause stress in animals,

Table 2. Microalgal Products and Meals Used in Aquaculture Feeds, Market Price, and Total Market Value[a]

Commercial product	Type	Origin	Approximate price (US$ kg^{-1})[vi]	Market size (US$ million)
Astaxanthin (10% purity)	Xanthophyll carotenoid	Petrochemicals (synthetic)	290	553.6 (2017)[vii]
		Haematococcus pluvialis (microalgae)	530	
Fucoxanthin (10% purity)		*Laminaria* sp. (macroalgae)	27	95 (2016)[viii]
β-Carotene (10% purity)	Carotene carotenoid	Petrochemicals (synthetic)	46	432.2 (2015)[ix]
		Blakeslea trispora (mold)	48	
		Dunaliella salina (microalgae)	65	
Phycocyanin (E18 grade)	Phycobiliprotein	*Spirulina* sp. (cyanobacteria)	160	112.3 (2018)[x]
DHA powder (>40% content)	Omega-3 fatty acid	*Schizochytrium* sp. (microalgae)	50	34 700 (2016)[xi]

[a]Prices were sourced from various suppliers on [vii] between September and December 2018.

sometimes reducing growth [67]. Consequently, there is considerable scope to improve the range and quality of alga-based oral therapeutic aquaculture feeds. Significant milestone studies in aquaculture for recombinant microalga-based oral therapeutics include: (i) increased survival of medaka fish that were fed with *Nannochloropsis oculata* expressing an active broad-spectrum antimicrobial peptide [69]; (ii) improved resistance to WSSV in shrimp that were fed with *D. salina* expressing WSSV antigens [70]; (iii) an improved immune response in juvenile rainbow trout following oral vaccination with *Chlamydomonas reinhardtii* expressing an antigen derived from *Renibacterium salmoninarum*, a causative agent of bacterial kidney disease [71]; and (iv) partial protection of shrimp against yellow head virus (YHV) after feeding on a transgenic alga expressing double-strand RNA against the virus [72].

Green Water Aquaculture

Freshwater fish (e.g., carp, tilapia) constitute the largest aquaculture sector [18] and thus are an important target for sustainable aquafarming practices. **Green water aquaculture** is an effective low-maintenance and low-cost technique used throughout Southeast Asia. Constructed ponds are fertilized (e.g., chemical, manure) to provide a 'nutritious soup' that promotes the growth of naturally occurring or inoculated algal populations and alga grazers (e.g., bacteria, fungi, protozoa, zooplankton), which together form nutrient-rich biomass [18]. The farmed animals directly graze on the available biomass, significantly reducing the reliance on commercial aquafeeds of fish and shrimp production [18]. Grazing, in conjunction with water recirculation systems and fertilization control, help to maintain a beneficial microbial composition and a healthy aquatic environment [18]. Some microalgae also supplement atmospheric CO_2 with organic carbon, which can ensure optimal C:N ratios in biomass, reduce biological oxygen demand, and maintain adequate dissolved organic nitrogen levels.

Low-water-exchange green water farming has enabled successful larval rearing of several commercially important Australian estuarine fish and crustaceans due to optimal nutrition, lower stress levels, improved environmental conditions (e.g., turbidity, light scattering, visual contrast), better water quality, the presence of chemical and digestive stimulants, and the beneficial bioactive properties of microalgae for the grown larvae [73]. Compared with clear water aquaculture, green water ponds have shown high inhibition of fish and shrimp pathogens [73]. For Asian tiger shrimp, substitution of fishmeal and oil with green water biomass reportedly yielded additional growth [74]. The benefits of green water appear to be the provision of a high-quality feed and probiotics and the fact that healthy ecosystems support disease suppression by preventing the proliferation of opportunistic pathogens [74,75].

It is estimated that 30% of global tilapia production is supplied using 'natural food' [18]. The quantity of microalgae consumed in 'green water' aquaculture has been estimated to be 240 million tonnes annually on a fresh-weight basis, more than the total aquaculture production [4,18].

Integrated Multitrophic Aquaculture Systems

Green water applications have significant scope to become a cornerstone of multitrophic integrated aquaculture (IMTA) systems [76], which can provide economic and environmental sustainability through cocultivation with **biofilter organisms** from different trophic levels (not only algae but also invertebrates; e.g., bivalves, sponges). These organisms can support circular nutrient flows in closed systems, and so water recycling and waste treatment, which incur significant costs to aquaculture. For example, a pilot facility in Australia used sand-filtered ponds stocked with polychaetes to remediate wastewater from adjacent shrimp production ponds. The polychaetes graze on phytoplankton grown on nutrient-rich wastewater, providing a simple, low-energy, efficient strategy to 'harvest' the microalgae by conversion into easily harvested animal biomass. Polychaetes are valuable sources of biomass as well as protein for animal feeds, thus creating a value chain incorporating shrimp, bioproducts, and low-cost water treatment [77].

Further large-scale integration of aquaculture with conventional agriculture (e.g., tilapia farming in rice paddy fields) [78] and aquaponics (e.g., cocultivating tilapia with lettuce) [79] may enable these benefits at the global scale, supporting a sustainable circular bioeconomy.

Biofloc Technologies in Aquafeeds

Expanding on the principles of green water farming, **biofloc** technologies are rapidly emerging as a sophisticated method of production of sustainable high-value 'biofloc meal' used in commercial aquafeeds [80]. Typically grown in closed photobioreactors, commercial feed suppliers are advancing understanding of the microbial ecosystems required to develop precise methods to produce biofloc-based, fish-free marine microbe feeds. Products entering the market include the Novacq™ biofloc supplement (grown on cheap agricultural waste) for salmon, barramundi, shrimp, and oysters [25]. Novacq™ reportedly increased shrimp growth by up to 50% compared with a standard reference diet of the same basic nutritional specifications [81]. Alternative biofloc products have also reported significant improvements in whiteleg shrimp (*Litopenaeus vannamei*) cultivation [82–84].

Concluding Remarks

Given the rapid expansion of the aquaculture sector, sustainable aquaculture feed solutions that form part of an expanding circular bioeconomy are required to enhance global sustainability. Microalgae have already been demonstrated to be a valuable source of key nutrients for high-quality fish feeds, including essential amino acids, omega-3 fatty acids, EPA and DHA, pigments, and antioxidants (e.g., carotenoids). Novel alga-based aquaculture feeds have the potential to completely replace fishmeal and fish oil; the current gold-standard, but unsustainable, feed source of the industry. Total global replacement of fishmeal with microalgae would reportedly require US$30 billion of capital and 111 000 ha of land, providing a net income of US$6.5 billion with the additional benefit of removing pressure on wild pelagic fish populations [85].

Analysis of the use of microalgae as whole-cell feeds, formulated feeds, animal health and growth supplements, and delivery systems for aquaculture therapeutics as well as biofloc-based feeds, IMTA systems, and green pond approaches shows significant opportunities for microalgae to

Outstanding Questions

How can nutrient composition and digestibility be improved for plant-based aquaculture feeds?

How can plant-based aquaculture feeds be made more effective, especially for carnivorous fish such as salmon?

How will the increasing demand for omega-3 oils affect the aquaculture feed market?

Which technologies and approaches can best drive down the cost of microalga production?

Can algal water treatment systems be coupled to aquafeed production to enable a circular industry?

Could advances in green pond technology permit increased sustainable production to meet future demands?

Would regulators permit oral alga-based vaccine feeds to prevent disease loss?

What policies can be implemented to increase the utilization of sustainably produced aquaculture feeds?

play a major role in aquaculture's 'blue revolution' and reduce its environmental footprint, including habitat destruction, water pollution, eutrophication, biotic depletion, ecological effects, and disease outbreaks. However, major advances are required, including the establishment of expanding algal collections for breeding purposes, their genome sequencing, identification of species and polyculture optima, and the development of systems that can support multitrophic and multilayered production. Significant additional advances are likely in feed formulations that enhance the microbiome, the organism, and system health and productivity. Substantial cost decreases through the discovery or engineering of low-cost technologies and nutritious strains with high digestibility, as well as the development of biorefinery approaches to maximize value from microalgal biomass, will allow full market adoption of microalga-based aquaculture feeds (see Outstanding Questions).

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Resources

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[ii]www.un.org/sustainabledevelopment/sustainable-development-goals/

[iii]https://stats.oecd.org/Index.aspx?DataSetCode=HIGH_AGLINK_2017

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