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REVIEW ARTICLE

Microalgae as fishmeal alternatives in aquaculture: current status, existing problems, and possible solutions

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Abstract
Fishmeal is an indispensable ingredient for most aquatic animals. However, the finite supply and escalating price of fishmeal seriously limit its use in aquaculture. Thus the development of new, sustainable protein ingredients has been a research focus. Microalgae are potential fishmeal alternatives owing to their high protein content and balanced amino acid profile. Studies suggest that suitable replacement of fishmeal with microalgae is beneficial for fish growth performance, but excessive replacement would induce poor growth and feed utilization. Therefore, this paper aims to review research on the maximum substitutional level of fishmeal by microalgae and propose the main issues and possible solutions for fishmeal replacement by microalgae. The maximum replacement level is affected by microalgal species, fish feeding habits, quality of fishmeal and microalgal meals, and supplemental levels of fishmeal in the control group. Microalgae could generally replace 100%, 95%, 95%, 64.1%, 25.6%, and 18.6% fishmeal protein in diets of carp, shrimp, catfish, tilapia, marine fish, and salmon and trout, respectively. The main issues with fishmeal replacement using microalgae include low production and high production cost, poor digestibility, and anti-nutritional factors. Possible solutions to these problems are recommended in this paper. Overall, microalgae are promising fishmeal alternatives in aquaculture.

Keywords Microalgae · Fishmeal substitution · Anti-nutritional factors · Heterotrophic culture · Aquaculture · Aquafeed

Introduction

Aquaculture is the fastest-growing food-producing sector in the world and the primary source of aquatic products for humans (Houston et al. 2020; Subasinghe et al. 2009). The rapid development of aquaculture depends heavily on the supply of aquafeed. It is estimated that the total compound aquafeed usage in aquaculture was 51.23 million tonnes in 2017, and is expected to rise to 73.15 million tonnes by 2025 (Tacon 2020). In fish farming, aquafeed generally represents approximately 50% to 70% of total aquaculture production costs (Foster et al. 1995; Vassiliou et al. 2015). Protein is the most expensive component in aquafeed (Craig and Helfrich 2009). Among various protein ingredients in aquafeed, fishmeal is regarded as the ideal protein source for most aquatic animals owing to its balanced amino acid profile and palatability (Jannathulla et al. 2019). However, the limited stock, unstainable growth, and unstable supply escalate the price of fishmeal (Abbott et al. 2021). Therefore, great efforts have been made to look for fishmeal alternatives (Glencross et al. 2007; Tacon et al. 2011; Teves and Ragaza 2016).

Microalgae, a diverse collection of O_2-evolving, photosynthetic organisms, are characterized by wide distribution, rapid growth and reproduction, and strong tolerance to extreme environments, etc. (Mata et al. 2010; Richmond and Hu 2013). Some microalgae are rich in protein (e.g., *Spirulina*) and could be effective solutions to the problem of fishmeal alternatives in aquaculture (Ahmad et al. 2022; Nagappan et al. 2021). Although many reviews have been done on applications of microalgae in aquaculture (Ahmad et al. 2020; Alagawany et al. 2021; Hemaiswarya et al. 2011; Ragaza et al. 2020; Tham et al. 2023), little attention

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was given to fishmeal replacement. Accordingly, the following discussion focuses on microalgal meals as fishmeal alternatives and summarizes advances as a basis for future improvements.

Current status of fishmeal production

Fishmeal is a brown powder obtained after cooking, pressing, drying, and milling fresh raw fish and byproducts derived from fish processing (Shepherd and Jackson 2013). Raw fishes used to manufacture fishmeal are mainly composed of small marine pelagic species (e.g., anchovy, mackerel, herring, and sardine) (Péron et al. 2010). Production of these raw fishes is easily affected by climate conditions (mainly El Niño Events). It is estimated that an El Niño year can decrease 4–5 million tonnes of raw fish and 1 million tonnes of fishmeal in Peru and northern Chile (Hardy 2010). Therefore, global fishmeal production fluctuates according to changes in the catches of these raw fish species and averages 5 million tonnes annually (Fig. 1). From 2001 to 2010, the average yearly fishmeal production was above 5.5 million tonnes, while from 2011 to 2020 it was around 5 million tonnes (European Commission 2021). According to FAO, global fishmeal production is expected to reach approximately 6 million tonnes in 2030 owing to an increased amount of the production being obtained from fish waste and byproducts of the processing industry (FAO 2020). Since fishmeal stocks are limited, and face growing sustainability concerns, the fishmeal price has been increasing dramatically for the last 20 years. According to FAO (2020), the fishmeal price is projected to reach 1800 USD/ton by 2030 (Fig. 1).

Aquaculture is the primary consumer of fishmeal (Boyd et al. 2022; Hua et al. 2019). No dramatic changes were made in the global fishmeal use by sector throughout 2009–2019 (Fig. 2). In 2009 and 2010, 63% and 73% of world fishmeal were consumed by aquaculture (Shepherd and Jackson 2013). In 2017–2019, the share increased up to 78% (European Commission 2021). In 2019, around 25% of the fishmeal going into aquaculture was used to feed crustaceans, 15% to feed salmon and trout, 17% to feed marine fish, and 21% to feed freshwater species. The rest was divided between tilapias, cyprinids, and eels (Fig. 2) (European Commission 2021). With the rapid growth of aquaculture, fishmeal could hardly meet the demands.

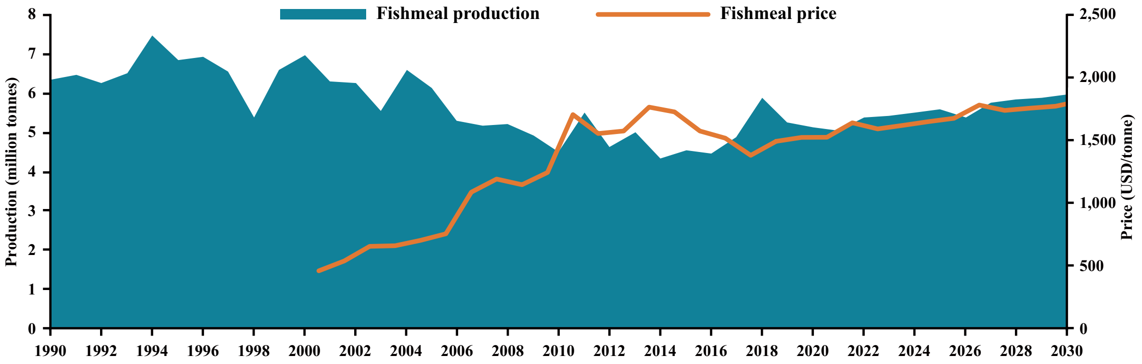

Fig. 1 Global production and price of fishmeal

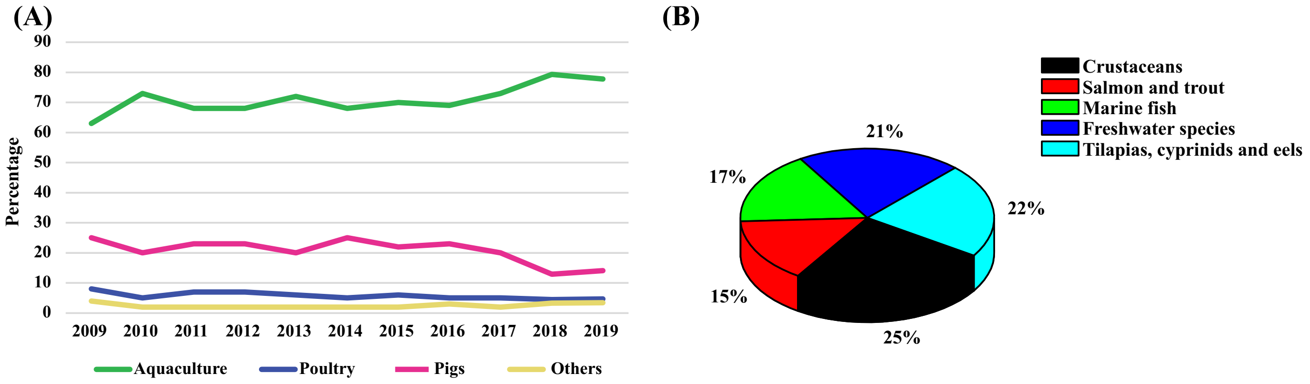

Fig. 2 Percentage of global fishmeal consumption by market sector (**A**), and the percentage of fishmeal in aquaculture consumption by aquatic animal type (**B**)

Current status of microalgal production

Microalgal production comprises several major stages: microalgae cultivation, dewatering, and drying (Fig. 3) (Halim et al. 2012). Microalgae cultivation is conducted in either open systems or closed systems (Chisti 2007). The commonly used open systems include circular ponds and raceway ponds; the closed systems contain tubular photobioreactors, flat plate photobioreactors, and fermenters (Perez-Garcia et al. 2011; Posten 2009). Both systems have advantages and disadvantages (Dębowski et al. 2020). The open systems have a lower production cost and operating cost but also have some disadvantages, including water evaporation, difficulties in managing culture conditions, poor microalgae growth, and susceptibility to microbial contamination (Goswami et al. 2021). On the other hand, the closed systems have higher cell densities and are easier to control culture conditions and microbial contamination, but have higher production and operating costs (Pulz 2001). Flocculation is regarded as the most advantageous dewater technology owing to its low energy requirement (Wijffels and Barbosa 2010). Spraying drying, drum drying, and freeze drying are common drying methods for obtaining microalgae biomass in microalgal production (Grima et al. 2013). Microalgae biomass applied in aquaculture could be classified into two categories: whole microalgae and lipid-extracted microalgae which are the protein-rich byproducts of diesel production from microalgae (Fig. 3) (Maisashvili et al. 2015; Sarker et al. 2018).

Presently, large-scale production of microalgae is dominated by several genera (e.g., *Spirulina* sp., *Chlorella* sp., *Dunaliella* sp., *Aphanizomenon* sp., *Haematococcus* sp., *Crypthecodinium* sp., and *Schizochytrium* sp.) (Rizwan et al. 2018). It is estimated that the annual production of microalgae ranged from 19,000 to 20,000 tonnes (dry weight) between 2016 and 2018, and was projected to increase up to 27,500 tonnes (dry weight) in 2024 (Benemann et al. 2018; Transparency Market Research 2016). Among the main microalgal species, *Spirulina* and *Chlorella* account for 65.78% and 26.32%, respectively (Fig. 4).

Microalgae as fishmeal alternatives

The high protein content and balanced amino acid profiles are considered the main reasons for microalgae as protein sources in aquafeed (Kovač et al. 2013). Microalgae can synthesize all amino acids, thus containing all the essential amino acids in significant amounts (Ibañez and Cifuentes

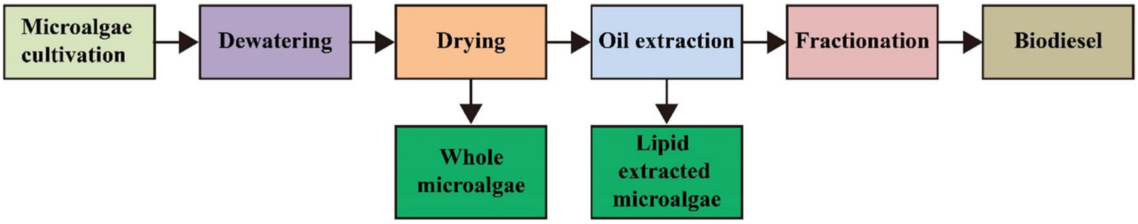

Fig. 3 Process flow diagram for diesel production from microalgae

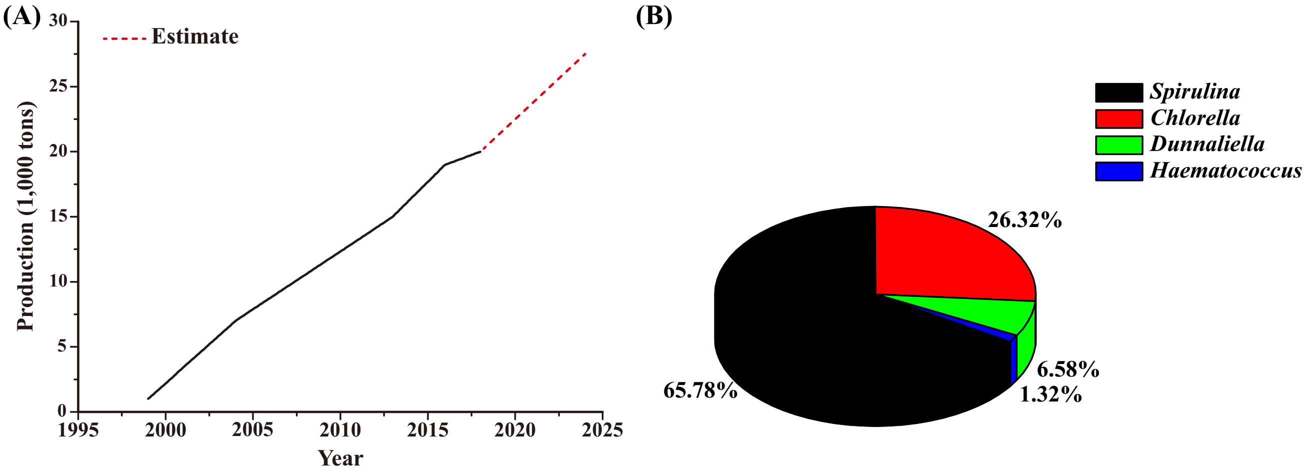

Fig. 4 Global microalgal production (**A**) and the proportions of the dominant genera involved

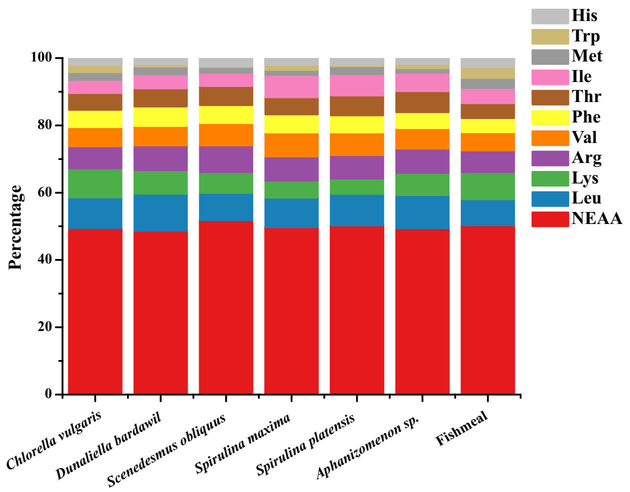

Fig. 5 Amino acid composition of microalgae (% total amino acids) (Becker 2007; Sauvant et al. 2004)

Table 1 General composition of some microalgae with great potential in replacing fishmeal (% dry weight) (Becker 2007; Roy and Pal 2015)

Microalga	Protein	Carbohydrate	Lipids
Anabaena cylindrica	43–56	25–30	4–7
Aphanizomenon flos-aquae	62	23	3
Chlamydomonas rheinhardii	48	17	21
Chlorella vulgaris	51–58	12–17	14–22
Chlorella pyrenoidosa	57	26	2
Dunaliella salina	57	32	6
Euglena gracilis	39–61	14–18	14–20
Scenedesmus obliquus	50–56	10–17	12–14
Spirulina maxima	60–71	13–16	6–7
Spirulina platensis	46–63	8–14	4–9
Synechococcus sp.	63	15	11

2013). The amino acid composition of the microalgae is similar, irrespective of algal class (Fig. 5), which suggests that protein quality also is similar (Brown et al. 1997). Besides, they also demonstrate the varying potential of digestibility, with digestibility coefficients ranging from 59.4% to 95.1% (Becker 2004b). It was suggested that the average protein quality of most microalgae could be superior to conventional plant feedstuffs (Becker 2007). *Spirulina* and *Chlorella* are rich in protein and possess great potential in fishmeal replacement in aquaculture (Alagawany et al. 2021). Besides *Spirulina* and *Chlorella*, there are some protein-rich microalgae with great potential to replace fishmeal, such as *Scenedesmus, Dunaliella*, and *Synechococcus* (Table 1).

Partial replacement of fishmeal with microalgae significantly increases feed intake and fish growth through bioactive compounds (e.g., pigments, vitamins, minerals, and fatty acids) in microalgae (Alagawany et al. 2021; Chen et al. 2021). However, accumulating studies suggest that excessive replacement would induce poor growth and feed utilization (Binh Van et al. 2020; Olvera-Novoa et al. 1998). Several aspects could account for the phenomenon. First, the high inclusion of *Spirulina* induces mineral deficiency, resulting in decreased biomass productivity (Olvera-Novoa et al. 1998). Minerals are essential for maintaining the normal life processes of aquatic animals (Lall 2022), and ash content in fishmeal is higher than that in *Spirulina* meal (Kim et al. 2013; Olvera-Novoa et al. 1998). Olvera-Novoa et al. (1998) found that the addition of phosphorus (P) in the 100% replacement group significantly increased fish growth and feed efficiency over groups without P addition in Mozambique tilapia (*Oreochromis mossambicus*), similar results were also found in gibel carp (*Carassis auratus gibelio*) (Cao et al. 2018a). Second, the high replacement of fishmeal by microalgal meals decreased feed palatability, leading to reductions in feed intake and fish growth (Walker and Berlinsky 2011). Fishmeal replacement with *S. maxima* meal increased feed hardness, decreasing the feed palatability and feed intake in Mozambique tilapia (Olvera-Novoa et al. 1998). Walker and Berlinsky (2011) utilized *Nannochloropsis* sp. and *Isochrysis* sp. to replace fishmeal in Atlantic cod (*Gadus morhua*) and also found a palatability problem in groups with excessive fishmeal replacement by microalga. Third, anti-nutritional factors (ANFs) in microalgae may inhibit fish growth when microalgae meals replace high levels of fishmeal (Ahmad et al. 2022). ANFs are known to inhibit fish growth and some ANFs have been reported in microalgae (National Research Council 2011; Silva et al. 2020; Jacob-Lopes et al. 2019). Therefore, in the present review, we concentrate on the maximum replacement level of fishmeal by microalgae meals without affecting fish growth performance.

Maximum replacement level of fishmeal with *Spirulina* meal

Spirulina is a multicellular, filamentous, photoautotrophic cyanobacteria that naturally lives in tropical and subtropical water bodies with high pH and alkalinity (Vonshak 1997). *S. maxima* and *S. platensis* are the two most studied *Spirulina* for fishmeal replacement in aquaculture (Table 2). As a fishmeal alternative, *Spirulina* has many advantages. Firstly, it contains high protein (60%-70% dry weight); secondly, *Spirulina* cells do not have cellulose walls, which makes their protein highly digestible (Altmann and Rosenau 2022; Ragaza et al. 2020). *Spirulina* has already been tested as a substitute for fishmeal protein source for many aquatic animals, including sturgeon, trout, carp, catfish, tilapia, prawn, and shrimp.

Research on *Spirulina* as a fishmeal alternative in sturgeons was mainly conducted by Palmegiano et al. (2005,

Table 2 Maximum replacement levels of fishmeal with *Spirulina* meals in aquatic animals

Microalga	Fish	Algae[a]	Fishmeal[b]	Relative[c]	Absolute[d]	Reference
Spirulina sp.	Siberian sturgeon (92.1 g)	0–60%	6–54%	88.9%	60% vs. 48%	Palmegiano et al. (2005)
Spirulina sp.	White sturgeon (17.5 g)	0–40%	20–54%	63%	40% vs. 34%	Palmegiano et al. (2008)
S. platensis	Rainbow trout (101 g)	0–10%	32–42%	23.8%	10% vs. 10%	Teimouri et al. (2013)
S. platensis	Common carp (20 g)	0–31%	0–25%	100%	31% vs. 25%	Nandeesha et al. (1998)
Spirulina sp.	Common carp (32.7 g)	0–20%	14.2–24.2%	41.2%	20% vs. 10%	Abdulrahman and Ameen (2014)
S. platensis	Gibel carp (5.0 g)	0–20%	0–19.8	100%	20% vs 19.8%	Cao et al. (2018a)
S. platensis	Giber carp (15.4 g)	0–13.5%	0–12%	100%	13.5% vs 12%	Cao et al. (2018b)
S. platensis	Catla and Rohu	0–31%	0–25%	100%	31% vs. 25%	Nandeesha et al. (2001)
S. platensis	African catfish (7.8 g)	0–18.8%	6.25–25%	75%	18.8% vs.18.8%	Raji et al. (2019)
Spirulina sp.	African catfish (58.1 g)	0–30%	0–30%	100%	30% vs. 30%	Raji et al. (2020)
S. platensis	Yellow catfish (3.1 g)	0–28.8%	0–30%	80%	23.0% vs. 24.0%	Liu et al. (2019)
S. platensis	Pabda catfish (0.52 g)	0–7.07%	23.46–31.28%	25%	7.07% vs. 7.82%	Akter et al. (2023)
Spirulina sp.	Mekong giant catfish (400 g)	0–28%	0–29%	100%	28% vs. 29%	Tongsiri et al. (2010)
S. platensis	Mullet (0.3 g)	0–39%	0–39%	69.2%	27% vs. 27%	Rosas et al. (2019)
S. platensis	Barramundi (9.2 g)	0–28%	42–70%	ESP40% RSP20%	28% vs. 28% 14% vs. 14%	Binh Van et al. (2020)
S. maxima	Mozambique tilapia (0.3 g)	0–52%	0–52%	40%	21% vs. 21%	Olvera-Novoa et al. (1998)
S. maxima	Red tilapia (2.5 g)	0–23.4%	22.4–32%	30%	23.4% vs. 9.6%	Rincón et al. (2012)
S. platensis	Nile tilapia (0.9 g)	0–48%	0–56.5%	75%	39% vs. 42.5%	Velasquez et al. (2016)
S. platensis	Hybrid red tilapia (0.2 g)	0–28%	0–25%	100%	28% vs. 25%	El-Sheekh et al. (2014)
Spirulina	Hybrid striped bass (10.6 g)	0–28.9%	13.7–27.4%	50%	28.9 vs.13.7%	Perez-Velazquez et al. (2019)
S. pacifica	Parrot fish (57 g)	0–26%	33–53%	37.7%	26% vs. 20%	Kim et al. (2013)
Spirulina sp.	Red drum (2.3 g)	0–28.9%	13.7–27.4%	50%	28.9 vs.13.7%	Perez-Velazquez et al. (2018)
Spirulina sp.	Silver seabream (1.5 g)	0–62%	0–54%	50%	32% vs. 27%	El-Sayed (1994)
S. platensis	Pacific whiteleg shrimp (0.7 g)	0–40%	0–40%	75%	30% vs. 30%	Macias-Sancho et al. (2014)
S. platensis	Pacific whiteleg shrimp (2.6 g)	0–30%	0–40%	100%	30% vs. 40%	Pakravan et al. (2017)
S. platensis	Giant tiger prawn	0–20%	15–35%	57.1%	20% vs. 20%	Sivakumar et al. (2018)
S. platensis	Giant river prawn (2.2 g)	0–25%	0–25%	100%	25% vs. 25%	Radhakrishnan et al. (2016)

[a] Algae denotes the supplemental level of microalgae in aquafeed

[b] Fishmeal represents the supplemental level of fishmeal in aquafeed

[c] Relative means the relative substitutional level of fishmeal by microalgae

[d] Absolute level is expressed as microalgae absolute inclusion level vs. fishmeal absolute substitution level

ESP, enzyme-treated *Spirulina* protein; RSP, raw *Spirulina* protein

2008). In 2005, Palmegiano et al. evaluated *Spirulina* sp. (60% crude protein) as fishmeal alternatives in Siberian sturgeon (*Acipenser baeri*) by setting three replacement levels (63.0%, 75.9%, and 88.9%) and found that sturgeon in the 88.9% replacement group exhibited higher final body weight (FBW) and protein efficiency ratio (PER), and lower feed conversion ratio (FCR) compared to the control ($P < 0.05$) (Palmegiano et al. 2005). In another trial with white sturgeon (*Acipenser transmontanus*), Palmegiano et al. (2008) reported that *Spirulina* sp. could replace 63% fishmeal (34% absolute content) in white sturgeon without adverse effects on specific growth rate (SGR), FCR, PER, and survival rate.

As for trout, Teimouri et al. (2013) investigated the effect of replacing fishmeal with *Spirulina* meal (62.0% crude protein) using four substitutional levels (6.0%, 11.9%, 17.9%, and 23.8%) on growth performance of rainbow trout (*Oncorhynchus mykiss*). After ten weeks of feeding, they observed that *Spirulina* sp. could replace 23.8% fishmeal (10% absolute content) without affecting FBW, weight gain rate (WGR), SGR, and FCR (Teimouri et al. 2013).

Several studies have been conducted on the effects of dietary *Spirulina* as a fishmeal alternative on the growth performance of carps. According to the study of Abdulrahman and Ameen (2014), common carp (*Cyprinus carpio*) were fed diets containing different substitutional levels (10.3%, 20.7%, 30.6%, and 41.2%) of fishmeal (about 68% crude protein) by *Spirulina* sp. (34% crude protein), and fish weight gain in the 41.2% replacement group (15.0 g) nearly doubled compared to the control (8.4 g). In addition, Nandeesha et al. (1998) evaluated *S. platensis* (54.5% crude protein) as a fishmeal substitute in common carp and concluded that *S. platensis* could replace 100% fishmeal without detrimental impacts on FBW, SGR, FCR, and PER. Similarly, Cao et al. conducted two studies to evaluate fishmeal replacement with *S. platensis* in gibel carp and found that *S. platensis* could replace 100% fishmeal without adverse effects on feed intake (FI), FBW, SGR, feed efficiency (FE), and PER (Cao et al. 2018a, 2018b). These results were in line with findings reported for two Indian major carps catla (*Catla catla*) and rohu (*Labeo rohita*) (Nandeesha et al. 2001).

Similar to carps, four kinds of catfish species were reported in fishmeal replacement by *Spirulina* meal. Akter et al. (2023) investigated fishmeal replacement with *S. platensis* by setting four substitutional levels (10%, 15%, 20%, and 25%) in pabda catfish (*Ompok pabda*) and found that *S. platensis* could replace 25% fishmeal (7.82% absolute content) and simultaneously increase FBW, WGR, and SGR. Raji et al. (2020) evaluated the effect of 100% fishmeal replacement with *S. platensis* and found that 100% fishmeal replacement significantly increased FBW, FI, SGR, and PER, and decreased FCR ($P < 0.05$) in African catfish (*Clarias gariepinus*). Similar results were also reported in Mekong giant catfish (*Pangasianodon gigas*) (Tongsiri et al. 2010). However, in yellow catfish (*Pelteobagrus fulvidraco*), *S. platensis* can only replace 80% fishmeal and 100% fishmeal replacement significantly decreased FBW, feeding rate (FR), SGR, and FE (Liu et al. 2019). Differences in catfish species may partially account for the phenomenon.

Similar to carps and catfish, four kinds of tilapia species were used to investigate *Spirulina* meal as fishmeal alternatives. In Mozambique tilapia, Olvera-Novoa et al. (1998) substituted fishmeal with *S. maxima* (66.86% crude protein) and found that microalgae could replace 40% fishmeal. In red tilapia fingerlings (*Oreochromis* sp.), Rincón et al. (2012) evaluated three substitutional levels (10%, 20%, and 30%) of fishmeal with *S. maxima* and found no significant difference in WGR, PER, and FE among all groups. In hybrid red tilapia (*O. niloticus* x *O. mossambicus*), *S. platensis* replaced 100% fishmeal, increased FBW, WGR, PER, and survival rate, and decreased FCR ($P < 0.05$) (El-Sheekh et al. 2014). In Nile tilapia (*O. niloticus*), Velasquez et al. (2016) evaluated four substitutional levels (30%, 47%, 75%, and 100%) of fishmeal (65.65% crude protein) by *S. platensis* (56.7% crude protein) and found that up to 75% fishmeal could be replaced by microalgae without adversely influencing FBW, SGR, and survival rate.

Different from results in carps and catfish, *Spirulina* replaces less fishmeal in mullet (*Mugil liza*), silver seabream (*Rhabdosargus sarba*), and barramundi (*Lates calcarifer*). In an eighty-day-feeding trial with juvenile mullet, the effect of *S. platensis* (61.61% crude protein) in replacing fishmeal on fish growth performance was evaluated with four substitutional levels (30.7%. 50.0%, 69.2%, and 100%) (Rosas et al. 2019). Fish in the 69.2% replacement group had similar FBW, WGR, SGR, FCR, and PER compared to the control ($P > 0.05$), while fish in the 100% replacement group showed a lower SGR, PER, and survival rate, and a higher FCR ($P < 0.05$) (Rosas et al. 2019). El-Sayed (1994) evaluated *Spirulina* sp. as protein source for silver seabream with four substitutional levels (25%, 50%, 75%, and 100%) and found that *Spirulina* sp. (61.88% crude protein) could only replace up to 50% fishmeal without negative effects on FBW, WGR, SGR, FC, and PER. In agreement with these results, raw *S. platensis* (64.1% crude protein) can only replace 20% fishmeal (14% absolute content) in barramundi. However, the substitutional level of fishmeal could be increased up to 40% when *S. platensis* was treated using cellulose and serine endo-peptidase, suggesting that these enzymes can improve the quality of *Spirulina* meal.

In studies of fishmeal replacement with *Spirulina* meal in Pacific whiteleg shrimp (*Penaeus vannamei*), Pakravan et al. (2017) and Macias-Sancho et al. (2014) incorporated the same amount of fishmeal in the control group (40%), used the similar quality of microalgal meals (68.0% vs. 66.9%), but drew different conclusions. The former found that microalgae could replace 100% fishmeal without adverse effects on FBW, SGR, FCR, and survival rate. However, the latter observed that 100% replacement induced lower FBW, WGR, SGR, and a higher FCR compared to the control (Macias-Sancho et al. 2014). Differences in fishmeal quality could be the main reason for the phenomenon. Pakravan et al (2017) used fishmeal with 51% crude protein, while Macias-Sancho et al. utilized fishmeal with 68.6% crude protein. Inclusion of the same content of microalgae substituted higher levels of inferior fishmeal than superior fishmeal.

Two prawn species were used for fishmeal replacement with *Spirulina* meal. Sivakumar et al. (2018) evaluated the growth performance of giant tiger prawn (*Penaeus monodon*) fed diets containing different substitutional levels (14.3%, 28.6%, 42.8%, and 57.1%) of fishmeal by *S. platensis*. After a sixty-day-feeding trial, they found that 28.6% and 42.8% fishmeal replacement significantly increased FI, SGR, and FE, while 57.1% fishmeal replacement significantly decreased PER without adverse effects on FI, FCR, and SGR (Sivakumar et al. 2018). Radhakrishnan et al. (2016) investigated the impact of fishmeal replacement with *S. platensis* (62.1% crude protein) on the growth performance of giant river prawn (*Macrobrachium rosenbergii*) and found that microalgae could replace 100% fishmeal without adverse effects on WGR and SGR.

In addition, *Spirulina* meal was also used to replace fishmeal in hybrid striped bass (*Morone crhysops* × *M. saxatilis*), parrot fish (*Oplegnathus fasciatus*), and red drum (*Sciaenops ocellatus*). The results showed that microalgae could replace 50% fishmeal in hybrid striped bass (Perez-Velazquez et al.

2019), 37.7% fishmeal in parrot fish (Kim et al. 2013), and 50% fishmeal in red drum without detrimental effects on WGR, SGR, FE, and PER (Table 2).

Maximum replacement level of fishmeal with *Chlorella* meal

Chlorella is a genus of unicellular green microalgae and is rich in protein (42%-58%), minerals, vitamins, and carotenoids (Oh et al. 2022; Safi et al. 2014a). Compared with *Spirulina*, *Chlorella* has a rigid cellulose-rich cell wall, which makes it difficult for the digestive enzymes of aquatic animals to access the cellular components (Kotrbáček et al. 2015; Yamada and Sakaguchi 1982) and thus greatly limits its application in fishmeal replacement in aquaculture. Many effective methods have been employed to disrupt the cell wall of *Chlorella* to increase the digestibility of protein (Becker 2007; Safi et al. 2014b). Similar to *Spirulina* meal, work on *Chlorella* meal as fishmeal alternatives was carried out in many aquatic animals, including freshwater fish (e.g., carps and tilapias), marine fish (e.g., red drum), and crustaceans (Table 3).

In freshwater fish, studies on *Chlorella* meal for fishmeal replacement were concentrated on zebrafish, (*Danio rerio*), crucian carp (*Carassius auratus*), largemouth bass (*Micropterus salmoides*), African catfish, and Nile tilapia. In zebrafish (Carneiro et al. 2020) and crucian carp (Shi et al. 2017), fishmeal can be 100% substituted by *Chlorella* meal without affecting FBW, WGR, SGR, and PER. In largemouth bass (*Micropterus salmoides*), *Chlorella* meal could replace 75% fishmeal (30% absolute content) without influencing fish growth and feed utilization (Xi et al. 2022); when the replacing level reached 100% (40% absolute content), FBW, WGR, SGR, FI, and FE were all significantly decreased (Xi et al. 2022).

African catfish with different body weight was used to evaluate the effect of *Chlorella* sp. (58% crude protein) as fishmeal alternatives. In the small fish (7.8 g), *C. vulgaris* (58% crude protein) significantly increased FBW, SGR, FI, and PER, and decreased FCR in fish fed 75% replacement level diets (Raji et al. 2019). In the big fish (58.1 g), only the 100% fishmeal replacement level was assessed and fish in the 100% replacement group by *C. vulgaris* (58% crude protein) had higher FBW, SGR, and PER, and lower FCR compared to the control ($P < 0.05$) (Raji et al. 2020).

Badwy et al. (2008) investigated the effect of *Chlorella* sp. (46.78% crude protein) as fishmeal alternatives with four replacement levels (10%, 25%, 50%, and 75%) in Nile tilapia and found that *Chlorella* sp. could only replace 50% fishmeal (11.11% absolute content). In a later study, juvenile Nile tilapia were fed diets in which fishmeal was replaced by *Chlorella* sp. (47.2% crude protein) using three substitutional levels (34.3%, 67.2%, and 100%) (Lupatsch and Blake 2013) and *Chlorella* sp. could only replace 34.3% fishmeal (22% absolute content) without adverse influence on growth performance. It is strange that the former replaced less absolute fishmeal but got a higher relative replacement level. The difference in replacement level could be mainly due to the fishmeal supplemental level in the control group. The former added 22.23% fishmeal, while the latter supplemented 64% fishmeal. Therefore, a higher supplemental level of fishmeal in the control group will decrease the relative substitution level of fishmeal by microalgae.

Table 3 Maximum replacement levels of fishmeal with *Chlorella* meals in aquatic animals

Microalga	Fish	Algae[a]	Fishmeal[b]	Relative[c]	Absolute[d]	Reference
Chlorella sp.	Zebrafish (0.2 g)	0–50%	0–50%	100%	50% vs. 50%	Carneiro et al. (2020)
Chlorella sp.	Crucian carp (1.8 g)	0–71%	0–53%	100%	71% vs. 53%	Shi et al. (2017)
C. vulgaris	African catfish (7.8 g)	0–18.8%	6.3–25%	75%	18.8vs. 18.8%	Raji et al. (2019)
C. vulgaris	African catfish (58.1 g)	0–30%	0–30%	100%	30% vs. 30%	Raji et al. (2020)
Chlorella sp.	Nile tilapia (6.5 g)	0–25.7%	5.6–22.2%	50%	17.1% vs.11.1%	Badwy et al. (2008)
Chlorella sp.	Nile tilapia (35 g)	0–78%	0–64%	34%	26% vs. 22%	Lupatsch and Blake (2013)
Lipid-extracted Chlorella sp.	Red drum (5.2 g)	0–43.7%	20.8–27.8%	10%	18.8% vs. 2.8%	Patterson and Gatlin (2013)
C. vulgaris	Olive flounder (104 g)	0–15%	54–60%	10%	15% vs.6%	Rahimnejad et al. (2017)
C. vulgaris	Gilthead seabream (1.1 g)	0–19%	37.6–53.7%	30%	19% vs. 16.1%	Karapanagiotidis et al (2022)
C. vulgaris	Largemouth bass (17.6 g)	0–47.5%	0–42%	75%	35.6% vs. 31.5	Xi et al. (2022)
C. vulgaris	Pacific whiteleg shrimp (2.6 g)	0–38.9%	0–40%	100%	38.9% vs. 40%	Pakravan et al. (2018)
C. vulgaris	Giant river prawn (2.2 g)	0–25%	0–25%	100%	25% vs. 25%	Radhakrishnan et al. (2015)

[a] Algae denotes the supplemental level of microalgae in aquafeed

[b] Fishmeal represents the supplemental level of fishmeal in aquafeed

[c] Relative means the relative substitutional level of fishmeal by microalgae

[d] Absolute level is expressed as microalgae absolute inclusion level vs. fishmeal absolute substitution level in aquafeed

Work on *Chlorella* meal for substitution of fishmeal in marine fish was mainly done in red drum, olive flounder (*Paralichthys olivaceus*), and gilthead seabream (*Sparus aurata*). In red drum, four substitutional levels (5%, 10%, 20%, and 25%) of fishmeal by lipid-extracted *Chlorella* sp. (21.2% crude protein) were assessed and only 5% and 10% fishmeal (2.8% absolute content) groups did not affect WGR, FE, and PER (Patterson and Gatlin 2013). However, the study on olive flounder (*Paralichthys olivaceus*) showed 10% fishmeal replacement (6% absolute content) by defatted *C. vulgaris* (57% crude protein) increased FBW, WGR, and SGR compared to the control ($P<0.05$) (Rahimnejad et al. 2017). Moreover, 30% fishmeal (16.1% absolute content) could be replaced in gilthead seabream without affecting fish growth performance (Karapanagiotidis et al. 2022).

Research on *Chlorella* meal as fishmeal alternatives in crustaceans was primarily conducted in Pacific whiteleg shrimp and giant river prawn. Pacific whiteleg shrimp were fed a diet in which fishmeal was replaced by *C. vulgaris* (51.5% crude protein) for eight weeks and showed no adverse effects on FBW, SGR, FCR, and survival rate in the 100% fishmeal replacement group (Pakravan et al. 2018). Similarly, Radhakrishnan et al. (2015) assessed the effect of dietary replacement of fishmeal with *C. vulgaris* (55.7% crude protein) on the growth performance of giant river prawn and observed that *C. vulgaris* could replace 100% fishmeal without influencing shrimp growth, survival rate, and feed utilization.

Maximum replacement level of fishmeal with *Scenedesmus* meal

Scenedesmus is a common freshwater green algal genera whose cells usually form flattened coenobia, arranged in linear or alternating series (Shubert and Gärtner 2015; Sucunthowong et al. 2023). *Scenedesmus* is easily cultured in the laboratory owing to its strong ability to adapt to harsh environmental conditions, simple nutritional requirements, and rapid growth rates (Lürling 2003; Trainor et al. 1976). At present, *Scenedesmus* has been used in many biotechnological applications due to its high nutritional content and bioactivities (Ishaq et al. 2016), including fishmeal replacement (Table 4). *Scenedesmus* possesses high protein content (50%-56%) (Becker 2007), contains all essential amino acids and a good amount of lipid and essential minerals (Geldenhuys et al. 1988), and its amino acid pattern could compare favorably with that of other food proteins (e.g., egg and soybean) (Becker 2004a). Compared to *Spirulina* and *Chlorella* meal, fewer aquatic animals were used to investigate the effect of *Scenedesmus* meal as fishmeal substitutes, including salmon and trout, tilapia, gilthead seabream, and spotted wolffish (*Anarhichas minor*) (Table 4).

S. almeriensis (46.7% crude protein) from an integrated system waste-nutrient was assessed in rainbow trout and induced significantly lower FBW, SGR, FI, PER, and FE in the 5% fishmeal replacement group (Tomas-Almenar et al. 2018). Similarly, *Scenedesmus* sp. (45.7% crude protein) induced lower WGR, SGR, and PER in Atlantic salmon (*Salmo sala*) compared to the control in the 75% fishmeal replacement group, but did not affect fish growth performance in the 50% fishmeal replacement group (Gong et al. 2019).

Badwy et al. (2008) made use of *Scenedesmus* sp. (51.17% crude protein) to replace fishmeal in Nile tilapia and found that replacing 50% fishmeal increased FBW, WGR, and SGR, while replacing 75% fishmeal significantly decreased FBW, WGR, SGR, and FI, but had no significant effects on FCR and PER.

Gilthead seabream (*Sparus aurata*) were fed diets containing different substitutional levels (15.7%, 23.4%, 31.2%, and 46.9%) of fishmeal by *S. almeriensis* (43.2% crude protein) and showed no significant difference in FBW, SGR, FCR, and PER among all treatments (Vizcaíno et al. 2014). Nevertheless, *S. obliquus* (45.7% crude protein) could replace only 15% fishmeal without negative effects on FBW, WGR, and SGR in spotted wolffish juveniles (Knutsen et al. 2019).

Maximum replacement level of fishmeal with other microalgal meals

In addition to these common microalgae, some other microalgae could be also utilized to replace fishmeal (Table 5).

Table 4 Maximum replacement levels of fishmeal with *Scenedesmus* meals in aquatic animals

Microalga	Fish	Algae[a]	Fishmeal[b]	Relative[c]	Absolute[d]	Reference
S. almeriensis	Rainbow trout (75 g)	0–10%	13.5–23.5%	< 5%	< 1%	Tomas-Almenar et al. (2018)
Scenedesmus sp.	Atlantic salmon (229 g)	0–20%	2.5–10%	50%	10% vs. 5%	Gong et al. (2019)
Scenedesmus sp.	Nile tilapia (6.5 g)	0–23.5%	5.6–22.2%	50%	15.6 vs. 11.1%	Badwy et al. (2008)
S. almeriensis	Gilthead seabream (8 g)	0–38.7%	27.4–51.6%	47%	38.7% vs. 24.2%	Vizcaíno et al. (2014)
S. obliquus	Spotted wolffish (140 g)	0–12%	68–80%	15%	12%vs.12%	Knutsen et al. (2019)

[a] Algae denotes the supplemental level of microalgae in aquafeed

[b] Fishmeal represents the supplemental level of fishmeal in aquafeed

[c] Relative means the relative substitutional level of fishmeal by microalgae

[d] Absolute level is expressed as microalgae absolute inclusion level vs. fishmeal absolute substitution level in aquafeed

These microalgae are mainly marine algae and are usually abundant in lipids and essential fatty acids, such as *Nannochloropsis* spp, *Phaeodactylum tricornutum*, *Tetraselmis*, and *Grammatophor* in EPA, *Isochrysis*, *Schizochytrium* in DHA, and *Nanofrustulum*, *Navicula*, and *Desmodesmus* for biodiesel production. As fishmeal alternatives, these microalgae were used in the form of either lipid-extracted algae or whole algae. Compared with *Spirulina*, *Chlorella*, and *Scenedesmu*s, these microalgae are inferior in fishmeal replacement and are mainly utilized as fishmeal alternatives in Atlantic salmon, Atlantic cod, Nile tilapia, common carp, European sea bass (*Dicentrarchus labrax*), turbot (*Scophthalmus maximus*), red drum, and Pacific whiteleg shrimp (Table 5).

Kiron et al. evaluated three kinds of microalgae as fishmeal alternatives and found that *Nanofrustlum* sp. (11.9% crude protein) (Kiron et al. 2012), *Tetraselmis* sp. (27.9% crude protein) (Kiron et al. 2012), and defatted *Desmodesmus* sp. (about 63% crude protein) (Kiron et al. 2016) could replace 5%, 5%, and 26.1% fishmeal without affecting FBW, SGR, FCR, PER, and survival rate in Atlantic salmon. Similarly, Sørensen et al. found that *P. tricornutum* (49% crude protein) (Sørensen et al. 2016) and defatted *Nannochloropsis oceania* (43% crude protein) (Sørensen et al. 2017) could replace 11% and 14.5% fishmeal in Atlantic salmon, respectively. However, in Atlantic cod, a microalgal mix (*Nannochloropsis* sp. and *Isochrysis* sp.) (42.1% crude protein) as protein sources decreased FBW, FI, and FE in the two substitutional levels (14.1% and 26.5%). The phenomena can be explained by differences in species of microalgae and fish and protein content in microalgae.

Nile tilapia and common carp can tolerate high levels of dietary microalgae. In Nile tilapia, *Nannochloropsis oculata* could replace 100% fishmeal (7% absolute content) and simultaneously increase FBW, WGR, and SGR compared to the control

Table 5 Maximum replacement levels of fishmeal with other microalgal meals in aquatic animals

Microalga	Fish	Algae[a]	Fishmeal[b]	Relative[c]	Absolute[d]	Reference
Nanofrustulum sp.	Atlantic salmon (170 g)	0–17.4%	25.2–28.0%	5%	8.7% vs. 1.4%	Kiron et al. (2012)
Tetraselmis sp.	Atlantic salmon (170 g)	0–7.4%	25.2–28.0%	5%	3.7% vs. 1.4%	Kiron et al. (2012)
Desmodesmus sp.	Atlantic salmon (167.6)	0–20%	51–69%	26.1%	20% vs. 18%	Kiron et al. (2016)
Phaeodactylum tricornutum	Atlantic salmon (324 g)	0–6%	47.6–53.6%	11%	6% vs. 6%	Sørensen et al. (2016)
Nannochloropsis oceania	Atlantic salmon (215 g)	0–20%	49.5–69%	14.5%	10% vs. 10%	Sørensen et al. (2017)
Nanofrustulum sp.	Common carp (11.0 g)	0–32.3%	9.6–16%	39.9%	32.3% vs. 6.4%	Kiron et al. (2012)
Tetraselmis sp.	Common carp (11.0 g)	0–17.1%	9.6–16%	39.9%	17.1% vs.6.4%	Kiron et al. (2012)
Nannochloropsis and *Isochrysis* sp.	Atlantic cod (40.7 g)	0–28.1%	37.4–50.9%	< 14.1%		Walker and Berlinsky (2011)
Nannochloropsis oculata	Nile tilapia (34.5 g)	0–14.2%	0–7%	100%	14.2% vs. 7%	Sarker et al. (2020)
Tetraselmis suecica and Tisochrysis lutea (2:1)	European sea bass (204 g)	0–18%	15–27.5%	45.4%	18% vs. 12.5%	Cardinaletti et al. (2018)
Nannochloropsis sp.	European sea bass (21.7 g)	0–15%	20.6–30%	31.3%	15% vs. 9.4%	Valente et al. (2019)
Nannochloropsis sp.	Guppy (58.1 mg)	0–15%	56–62%	15%	15% vs. 6%	Sultana et al. (2022)
Lipid-extracted Nannochloropsis salina	Red drum (13 g)	0–13.4%	23.9–28.2%	< 5%		Patterson and Gatlin (2013)
Navicula sp.	Red drum (1.9 g)	0–20.6%	25–27.8%	10%	20.6% vs. 2.8%	Patterson and Gatlin (2013)
Lipid-extracted Navicula sp.	Red drum (1.9 g)	0–30%	25–27.8%	< 5%		Patterson and Gatlin (2013)
Nannochloropsis sp.	Turbot (24.6 g)	0–10%	42.3–50%	15%	10% vs. 7.7%	Qiao et al. (2019)
Haematococcus pluvialis	Pacific whiteleg shrimp (1 g)	0–12%	7.5–15%	50%	12% vs. 7.5%	Ju et al. (2012)
Nanofrustulum sp.	Pacific whiteleg shrimp (2.2 g)	0–35.5%	9.31–15.2%	40%	35.5% vs. 6.21%	Kiron et al. (2012)
Tetraselmis sp.	Pacific whiteleg shrimp (2.2 g)	0–17.0%	9.31–15.2%	40%	17.0 vs. 6.21%	Kiron et al. (2012)
Schizochytrium sp.	Pacific whiteleg shrimp (0.1 g)	0–28%	37–40.8%	9.1%	28% vs. 3.7%	Pacheco-Vega et al. (2018)
Grammatophora sp.	Pacific whiteleg shrimp (0.1 g)	0–36%	37–40.8%	9.1%	36% vs. 3.8%	Pacheco-Vega et al. (2018)

[a] Algae denotes the supplemental level of microalgae in aquafeed

[b] Fishmeal represents the supplemental level of fishmeal in aquafeed

[c] Relative means the relative substitutional level of fishmeal by microalgae

[d] Absolute level is expressed as microalgae absolute inclusion level vs. fishmeal absolute substitution level in aquafeed

(Sarker et al. 2020). Two substitutional levels (25% and 39.9%) of fishmeal by *Nanofrustlum* sp. (11.9% crude protein) and *Tetraselmis* sp. (27.9% crude protein) were evaluated in common carp and the results showed that both microalgae could replace 39.9% fishmeal (6.4% absolute content) without affecting WGR, SGR, FI, FCR, PER, and survival rate (Kiron et al. 2012).

European sea bass were fed diets containing three substitutional levels (15%, 30%, and 45%) of fishmeal by *Tetraselmis suecica* (48.7% crude protein) and *Tisochrysis lutea* (46.3% crude protein) (Cardinaletti et al. 2018). The microalgae mix (*T. lutea*:*T. suecica* = 2:1) could replace 45% fishmeal without (12.5% absolute content) affecting FBW, SGR, FCR, and PER (Cardinaletti et al. 2018). Moreover, lipid-extracted *Nannochloropsis* sp. (45.2% crude protein) could replace 31.3% fishmeal (9.4% absolute content) without influencing FBW and FCR in European sea bass (Valente et al. 2019), in agreement with results reported by Qiao et al. who found that *Nannochloropsis* sp. (50.72% crude protein) could replace up to 15.5% fishmeal (7.7% absolute content) in juvenile turbot (Qiao et al. 2019).

Patterson and Gatlin (2013) assessed three microalgae as fishmeal alternatives in juvenile red drum and found that fish fed diets in which 5% fishmeal replacement by lipid-extracted *Nannochloropsis salina* and lipid-extracted *Navicula* sp. had a lower WGR compared to the control, while whole *Navicula* sp. could replace 10% fishmeal without negative effects on WGR, FE, and survival rate. The quality of microalgae could partly explain the difference in fishmeal replacement by whole *Navicula* sp. and lipid-extracted *Navicula* sp. Whole *Navicula* sp. contained 19.4% crude protein and 18.8% crude lipid, while the lipid-extracted *Navicula* sp. possessed 13.3% crude protein and 4.9% crude lipid (Patterson and Gatlin 2013). Microalgae with higher protein levels generally substitute more fishmeal than those with lower protein content.

Five kinds of microalgae were used to replace fishmeal in Pacific whiteleg shrimp. *Nanofrustlum* sp. (11.9% crude protein) and *Tetraselmis* sp. (27.9% crude protein) could replace 40% fishmeal without influencing WGR, SGR, FI, FCR, PER, and survival rate (Kiron et al. 2012). Defatted *H. pluvialis* (40.3% crude protein) could replace 50% fishmeal without adverse effects on FBW, WGR, SGR, and survival rate, and significantly increased PER and FE compared to the control (Ju et al. 2012). *Schizochytrium* sp. (9.09% crude protein) and *Grammatophora* sp. (7.12% crude protein) could replace 9.1% fishmeal without adverse effects on FBW, WGR, SGR, and survival rate (Pacheco-Vega et al. 2018).

Summary of fishmeal replacement by microalgal meals

The maximum substitution level of fishmeal by microalgae was affected by several factors.

The first is the microalgal species. In general, maximum replacement levels of fishmeal were the highest in *Spirulina*, and the lowest in other microalgae (Tables 2, 3, 4, and 5). Protein content and protein digestibility in microalgae could partially explain the phenomenon. *Spirulina* meal generally has a much higher protein content, and its protein is more digestible because its peptidoglycan cell walls are much softer and more digestible for most fish than cellulose-based cell walls (e.g., *Chlorella*) (Teuling et al. 2017).

The second is the fish species and feeding habits. Carnivorous fish (such as salmon and trout) generally has lower maximum substitution level than omnivorous fish (e.g., tilapia, carps, crustacean, and catfish). Kiron et al. (2012) evaluated two marine microalgae (*Nanofrustulum* and *Tetraselmis*) as fishmeal alternatives in Atlantic salmon and common carp and found that two marine microalgae could replace over 40% fishmeal (6.21–6.39% absolute content) in common carp, but just 5% fishmeal (1.4% absolute content) in Atlantic salmon. Feeding habits or striking morphological and physiological differences in their digestive tracts could partially account for the phenomena (Kamalam et al. 2017). Carbohydrates are important components of microalgal biomass composition (Markou et al. 2012). The ability to use carbohydrates in fish are determined by their natural feeding habits (Kamalam et al. 2017). Atlantic salmon are carnivorous and cannot tolerate high amounts of carbohydrates (Krogdahl et al. 2003; Torstensen et al. 2008), whereas common carp are omnivorous and can digest substantial amounts of carbohydrates from plants (Kiron et al. 2012; Stone 2003).

Other factors include the difference in fishmeal quality, the supplemental level of fishmeal in the control group, and microalgal meal quality, which have been discussed in the previous sections.

Based on the results in studies with upper limits of the relative substitutional level of fishmeal (Supplemental Table), we made a summary of fishmeal replacement by microalgae. Microalgae could generally replace 100% (30.8% absolute content), 95% (28.3% absolute content), 95% (32% absolute content), 64.1% (20% absolute content), 25.6% (11.1% absolute content), and 18.6% (4.5% absolute content) fishmeal protein in carp, shrimp, catfish, tilapia, marine fish, and salmon and trout, respectively (Fig. 6). Nowadays marine fish and carnivorous fish (e.g., salmon and trout) are major consumers of fishmeal (Oliva-Teles et al. 2015), thus more attention should be paid to these species in future studies. Although a positive linear relationship exists between the relative substitutional level and the absolute substitutional level of fishmeal (Fig. 6), the absolute substitution level seemed to be a more reliable indicator than the relative substitution level due to huge differences in fishmeal supplemental level in the control group.

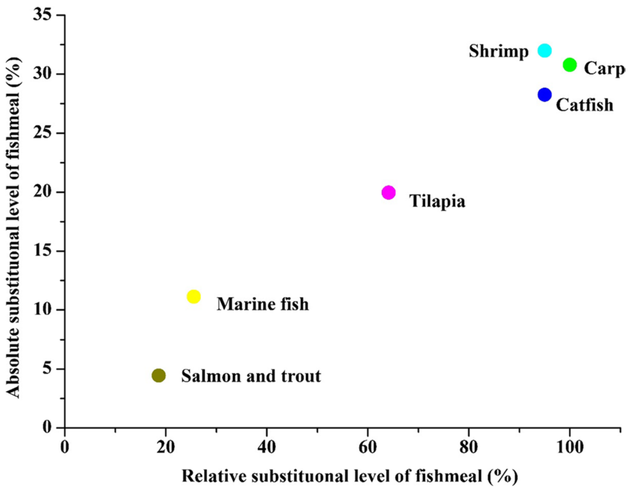

Fig. 6 Relationship between the relative and absolute substitutional levels of fishmeal by microalgal meals in aquatic animals

Main problems and possible solutions of microalgal meals in fishmeal replacement

Low production and high production cost

At present, the global autotrophic microalgae biomass production is about 20,000 tonnes (dry weight) (Benemann et al. 2018), while the annual production of fishmeal used in aquaculture is estimated to be 3,900,000 tonnes (European Commission 2021). Therefore, the huge gaps in production at present cannot be filled. Moreover, microalgal production costs are much higher than fishmeal. Presently, the production cost of *Spirulina* and *Chlorella* meal ranges from about 10 USD/kg to 30 USD/kg (Benemann et al. 2018). However, the maximum price of fishmeal achieved in 2013 was just 1.74 USD/kg. Thus the price difference makes it impossible for fishmeal replacement by microalgal meals at present.

Heterotrophic culture seems an effective solution to these problems. Heterotrophic culture occurs in a closed fermentation process that uses organic carbon sources for microalgal growth in the absence of light. Compared to the most commonly used autotrophic cultivation of microalgae, heterotrophic cultivation is much cheaper, simpler in construct facilities, easier to maintain on a large scale, and higher in cell densities (up to 100 g/L in heterotrophic vs. 0.5–2 g/L in autotrophic) (Barclay et al. 2013; Chen 1996; Perez-Garcia et al. 2011). Presently, some microalgae have been achieving commercial success via fermentation, such as *Chlorella*, *Crypthecodinium*, and *Schizochytrium* (Barclay et al. 2013). Although the protein content of heterotrophic cells (10.3–25.8%) was much lower than that of autotrophic cells (up to 52.6%), an over-compensation strategy (Xie et al. 2017) and a novel two-stage heterotrophic cultivation for starch-to-protein method (Xiao et al. 2022) have been used to increase the protein content of heterotrophic *Chlorella* which could be comparable in protein content to that cultured under autotrophic conditions. Furthermore, efforts in the improvement of the algal medium, culture facility, and harvesting methods are necessary to increase global microalgal production. Improvements in harvesting methods could reduce the production cost of microalgal meals to some extent since microalgal harvesting accounts for 30% of the total production cost for microalgae (Yang et al. 2021).

Poor digestibility

Poor digestibility of microalgae was mainly associated with their high content of carbohydrates which are mainly starch (cell content) and non-starch polysaccharides (NSP) (cell wall) (de Farias Silva and Bertucco 2016; Maia et al. 2020; Velazquez-Lucio et al. 2018).

The ability to utilize starch in fish varies in species and is affected by many aspects, such as fish feeding habits (mainly variations in the anatomical structure and function of the gastrointestinal tract), dietary starch levels, starch sources, processing conditions of starch, and rearing conditions (Krogdahl et al. 2005). Generally, carnivorous fish have a lower ability to utilize starch than herbivorous and omnivorous fish (Krogdahl et al. 2005; Polakof et al. 2012). Yamamoto et al. (2001) compared the starch digestibility in common carp and rainbow trout and found that the starch digestibility in common carp and rainbow trout was 90% and 78%, respectively.

NSPs are predominantly structural components of cell walls, comprising cellulose, β-glucans, hemicellulose, pectins, and gums (National Research Council 2011; Sinha et al. 2011). NSPs in microalgal cell wall includes cellulose, hemicellulose, and pectins (Domozych et al. 2012, 2007; Scholz et al. 2014). NSPs are considered to be unavailable as energy sources for the majority of fish due to the absence of adequate gut microbiota for their digestion and the lack of specific NSP-degrading digestive enzymes (Maas et al. 2020; Polakof et al. 2012; Sinha et al. 2011). The presence of NSPs in aquafeed has induced adverse effects on feed utilization and fish growth (Sinha et al. 2011). Sarker et al. (2018) evaluated the substitution of fishmeal with lipid-extracted *N. oculata* in diets of Nile tilapia and attributed the growth retardation of fish in the high fishmeal substitution group to high levels of cellulose (3.7%) and hemicellulose level (43.3 ug/mg) in microalgae.

Several solutions can be adopted to address the digestibility problem in microalgae. Firstly, physical treatment (e.g., bead milling and freezing) (Velazquez-Lucio et al. 2018) or enzymatic digestion (addition of NSP-degrading enzymes) (Córdova et al. 2019) could be used to alleviate the adverse effects of NSPs. Compared to the control (without disruption), disruption of the cell wall in *Nannochloropsis gaditana* by bead milling improved protein digestibility, weight gain, and feed utilization by 16.3%, 13%, and 11%, respectively, in African catfish

Table 6 Potential anti-nutritional factors (ANFs) in microalgae

ANFs	Contents of ANFs	Microalgae	References
Tannins	2.02 mg/g	*Spirulina platensis*	Hetta et al. (2014)
	6.58 mg/g	*Spirulina* sp.	Wu et al. (2005)
	18.1 mg/g	*S. platensis*	Kavisri et al. (2021)
	1.44 mg/g	*Chlorella* sp.	Wu et al. (2005)
	0.49–1.72 mg/g	*C. vulgaris*	El-fayoumy et al. (2020)
	23.2 mg/g	*C. vulgaris*	Prabakaran et al. (2018)
Alkaloids	71.6 mg/g	*C. vulgaris*	Prabakaran et al. (2018)
	89.5 mg/g	*S. platensis*	Kavisri et al. (2021)
Lectin	–	*S. acutus*	Silva et al. (2020)
	–	*Chlorella*	Jacob-Lopes et al. (2019)
	19.0 HU/mg	*N. oculata*	Sarker et al. (2018)
	240.0 HU/mg	Lipid-extracted *N. oculata*	Sarker et al. (2018)
Protease inhibitors	–	*C. vulgaris*	Sheih et al. (2009)
	1000 TIU/g (Trypsin inhibitors)	*N. oculata*	Sarker et al. (2018)
	2145 TIU/g (Trypsin inhibitors)	Lipid-extracted *N. oculata*	Sarker et al. (2018)

– denotes that the exact content was not given

(Agboola et al. 2019). Treatment with cellulose, β-glucosidase, and hemicellulose was proved effective in damaging the cell wall and releasing cellular organic compounds of *C. sorokiniana* (Córdova et al. 2019). Secondly, some starch in microalgae can be separated before the use of microalgal biomass as aquafeed ingredients. The aqueous two-phase system (ATPS) is considered a potential scalable method to isolate starch from other cellular components in microalgae after cell wall disruption (Di Caprio et al. 2022; Suarez Ruiz et al. 2020).

Anti-nutritional factors (ANFs)

ANFs refer to endogenous substances present in food and feedstuffs that adversely affect health and nutrition when ingested by humans and animals (Gemede and Ratta 2014). The detrimental effects induced by prolonged ingestion of ANFs include disturbance of digestive processes and growth, decreased feed intake and feed utilization, pancreatic hypertrophy, hypoglycemia, liver dysfunctions, and suppression of immunity (National Research Council 2011). ANFs in plants include tannins, phytate, oxalate, saponins, lectins, alkaloids, protease inhibitors, and cyanogenic glycosides (Francis et al. 2001; Gemede and Ratta 2014). Some ANFs have been reported in microalgae (Table 6), such as lectin in *Scenedesmus acutus* (Silva et al. 2020) and *Chlorella* (Jacob-Lopes et al. 2019). Lectin could disrupt the small intestinal metabolism and induce morphological damage to the villi (Francis et al. 2001). Diets containing tannins, alkaloids, or protease inhibitors have been proven to reduce feed intake and fish growth (de la Higuera et al. 1988; Mukhopadhyay and Ray 1999; Shiau et al. 1987). Adverse effects induced by these ANFs are similar to those when microalgae replace high fishmeal in aquatic animals. However, the direct relationship between these is unknown. Whether these adverse effects are induced by ANFs in microalgae needs further investigation.

Heat treatment (such as autoclaving) or treatment with chemical reagents (such as alkali) are suggested to reduce the content of tannins, alkaloids, lectin, and protease inhibitors (Francis et al. 2001; Samtiya et al. 2020). However, more care should be taken to minimize the loss of nutrients of microalgae in the treatment. Moreover, breeding for microalgae with low content of these ANFs could be an ideal solution (Sims et al. 2019).

Conclusion

In summary, microalgal meals could partially or completely replace fishmeal, with levels of substitution ranging from 0 to 100%. The maximum replacement level is affected by microalgal species, fish feeding habits, quality of fishmeal and microalgal meals, and supplemental levels of fishmeal in the control group. Generally, microalgae could replace 100%, 95%, 95%, 64.1%, 25.6%, and 18.6% fishmeal protein in diets of carp, shrimp, catfish, tilapia, marine fish, and salmon and trout, respectively.

The main problems and possible solutions concerning the application of microalgal meals in fishmeal replacement were proposed. Firstly, heterotrophic cultures and improvement of the algal medium, culture facility, and harvesting methods could increase production and decrease the production cost of microalgae. Secondly, physical treatment, enzymatic digestion, and starch separation could improve the poor digestibility of microalgae. Thirdly, heat treatment (such as autoclaving), treatment with chemical reagents, and breeding could decrease the ANFs in microalgae.

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Data availability The data that support the findings of this study are available from the corresponding author upon reasonable request.

Declarations

Competing interests The authors have no relevant financial or non-financial interests to disclose.

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