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HARNESSING GREEN MACROALGAE FOR SUSTAINABLE FISH FEED: OPPORTUNITIES AND CHALLENGES

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Abstract

The world faces a critical challenge in ensuring sufficient food production to meet the needs of a growing global population while maintaining nutritional quality and promoting environmental sustainability. Among sustainable food sources, seaweed, particularly the genus Ulva, has emerged as a promising solution due to its nutritional composition, abundance, and accessibility. However, integrating Ulva into animal feeds presents challenges, including nutritional value variability and indigestible polysaccharides, which reduce energy availability. This review explores the potential of Ulva sp. as an ecological and nutritious ingredient for aquaculture. It highlights the need for optimized nutritional strategies and processing technologies to increase protein content and improve nutrient digestibility. The actual status of the biochemical composition of Ulva and its benefits in commercial fish feed are emphasized, focusing on fish growth performance, stress resistance, immune function, and gut microbiota health. Drawing on over 50 studies, the review underscores positive trends. It identifies optimal inclusion levels for Ulva in fish diets, aiming to enhance digestibility and functional properties while addressing sustainability goals in aquaculture.

Key words: *functional compounds, nutritional, Ulva.*

INTRODUCTION

By 2050, population growth and climate change will exert considerable pressure on global food security, requiring sustainable solutions (Molotoks et al., 2021). Aquaculture plays a key role in this context, providing a sustainable alternative for protein supply and supporting responsible economic development. The integration of ecological principles in this industry contributes to the protection of aquatic ecosystems and the conservation of natural resources, reducing the impact on the terrestrial environment (Ahmed et al., 2019; Choudhary et al., 2021).

Aquaculture has emerged as one of the fastest-growing sectors in food production, providing an essential source of protein (Anderson et al., 2017). As this sector develops, the demand for feed has increased significantly, highlighting the need to identify alternative protein sources amid the declining availability of animal-based options (Aragão et al., 2022). Marine algae offer a promising solution due to their high nutritional value and environmental benefits, making them a viable alternative to conventional feed ingredients (Pereira et al., 2024). A well-balanced diet is crucial for ensuring the optimal health, growth, and productivity of farmed fish. However, the aquaculture industry's heavy reliance on fishmeal as the primary protein source raises significant sustainability concerns. These challenges stem from the depletion of wild fish stocks, the rising global demand for fishmeal, and the escalating costs associated with its production and procurement (Jannathulla et al., 2019). As a result, researchers and industry stakeholders are actively exploring alternative, more sustainable protein sources, to reduce dependence on fishmeal while maintaining fish health and performance.

Green algae, such as *Ulva lactuca*, stand out for their rich nutrient profile and bioactive compound content, offering significant potential for the development of functional diets for aquaculture fish (Holdt & Kraan, 2011).

Recent studies highlight that functional metabolites of seaweeds not only support growth performance but also enhance immunity, boost antioxidant status, and increase disease resistance, thus contributing to the maintenance of fish health (Aragão et al., 2022; Mota et al., 2023). However, there have been studies indicating that high levels of inclusion could lead to less efficient utilization of feed due to limited digestibility and nutrient uptake, which would negatively affect the growth rate (Wan et al., 2019; Pratiwi & Pratiwy, 2022).

In this context, the present study analyzes the nutritional properties and bioactive compounds found in seaweed, emphasizing their potential benefits for the growth, health, and overall welfare of farmed fish. Additionally, the paper explores strategies for improving seaweed processing methods to enhance its nutritional value while minimizing any potential adverse effects associated with its inclusion in aquaculture feed.

MATERIALS AND METHODS

This review comprises literature obtained from recognized academic databases such as Web of Science, Scopus, PubMed and Google Scholar.

The search strategy incorporated Boolean operators (AND, OR) and MeSH terms to refine results. Keywords and phrases used included: “green macroalgae”, “fish nutrition”, “growth performance”. “feed utilization”, “bioactive compounds”, “Ulva in aquaculture”, “immunostimulants”, “marine-derived polysaccharides”.

The selection of studies was based on predefined inclusion and exclusion criteria to ensure the relevance and quality of the data analyzed. Studies were included if they were published in peer-reviewed journals within the last two decades and provided experimental research, systematic reviews, or meta-analyses related to the utilization of macroalgae in aquafeeds. Only studies that contained information on nutritional composition, bioactive compounds, fish growth performance, immune response, or processing techniques for improving macroalgae digestibility were considered. In contrast, studies were excluded if they lacked experimental validation, were limited to theoretical discussions, or focused solely on microalgae or other non-macroalgal marine resources. Additionally, research with insufficient sample size or statistical significance was omitted.

RESULTS AND DISCUSSIONS

Optimizing production of macroalgae

Throughout history, macroalgae have been prized for their nutritional value, and are still part of the Asian diet today for their multiple health benefits (Hafting et al., 2015). However, with the intensification of studies on the macroalgae composition and on their bioactive compounds, the exploitation has registered a significant expansion globally (Dominguez & Loret, 2019; Kidgell et al., 2019). In this context, to ensure sustainable production, the optimization of harvesting and cultivation methods is essential for enhancing production of bioactive compounds. The availability and nutritional composition of Ulva biomass in natural stocks are influenced by a range of dynamic factors, including species and strain diversity, environmental conditions, associated microbiome, geographical location, and seasonal variations (Table 1). These fluctuations present significant challenges in ensuring the consistent quality and optimal utilization of Ulva as a sustainable resource for aquaculture and other applications.

Table.1 Nutritional composition of various species of Ulva

Species	Carbohydrates (%dw)	Proteins (%dw)	Lipids (%dw)	Ash (%dw)	References
Ulva lactuca	58.1	13.6	0.19	11.2	(Rasyid, 2017)
Ulva lactuca	54.95 ±1.43	14.58±1,30	0.69±0.06	18.38±3.08	(Sirbu et al., 2020)
Ulva lactuca	61.83 ± 0.01	10.0 ± 0.01	0.13 ± 0.01	17.86 ± 0.87	(Pangestuti et al., 2021)
Ulva rigida	31.87 ± 0.26	27.11 ± 0.62	2.71 ± 0.70	19.63 ± 0.63	(Kumar et al., 2021)
Ulva rigida	27.9±0.4	19.5±0.1	0.08±0.004	26.6±0.4	(Nova et al., 2023)
Ulva fasciata	545.301	38.897	0.1878	204.842	(Anis et al., 2018)
Ulva fasciata	32.0 ±0.04	22.7 ± 0.22	0.89 ± 0.12	27.0 ± 0.024	(Ganesan et al., 2020)

Species	Carbohydrates (%dw)	Proteins (%dw)	Lipids (%dw)	Ash (%dw)	References
Ulva reticulata	46.9 ± 0.56	9.86 ± 0.67	0.28 ±0.45	2.70 ± 0.32	(Jayasinghet et al., 2019)
Ulva reticulata	48.40±0.0	12.93±0.08	3.04±0.07	23.32±0.02	(Djoh et al., 2024)
Ulva intestinalis	57.03 ± 1.36	13.55 ± 0.07	2.72 ± 0.28	19.01 ± 1.15	(Jannat-Alipour et al., 2019)
Ulva intestinalis	5.16 ± 0.04	3.32 ± 0.14	0.04±0.01	5.62 ± 3.20	(Farzanah et al., 2022)
Ulva pertusa	-	15.4 ± 0.9	4.8 ± 2.9	27.2 ± 1.7	(Benjama & Masniyom,2011)
Ulva pertusa	52.3	25.1	0.1	22.5	(Lee et al., 2014)
Ulva clathrata	-	20.1 ± 0.1	2.2 ± 0.1	27.5 ± 0.2	(Peña-Rodríguez et al., 2011)

These factors directly impact both the yield and the overall availability of Ulva resources (Simon et al., 2022). Consequently, sustainable harvesting practices are crucial to prevent overexploitation and reduce environmental impact. However, some studies suggest that natural Ulva stocks may not be sufficiently productive for large-scale commercial harvesting, and the seasonal fluctuations in biomass make it challenging to accurately estimate production, ultimately affecting the ability to meet commercial demands (Calheiros et al., 2021).

Algaculture presents a viable and sustainable alternative for meeting industrial algae demands, particularly when natural harvesting becomes insufficient due to low biomass availability or inconsistent quality (Yong et al., 2022). By providing controlled cultivation conditions, algaculture ensures a more reliable and scalable supply of high-quality Ulva biomass, reducing dependence on wild stocks and supporting long-term sustainability.

To ensure a sustainable and environmentally friendly source of biomass, the macroalgae Ulva are cultivated in various types of systems. Seaweed culture systems can be realized offshore (open sea method), on land (onshore), where conditions are controlled, or close to the coast (nearshore), the latter being the most widely used aquaculture technique in estuaries and coastal areas (García-Poza et al., 2020). Beyond the simplistic approach of seaweed culture as a single production, seaweed can be integrated into a multitrophic aquaculture system (IMTA). *Ulva lactuca* cultivated in this system maintains a stable nutritional profile throughout the year, ensuring constant quality (Hayashi et al., 2014; Marinho-Soriano, 2017; Laramore et al., 2022).

Establishing an ideal protocol for obtaining the best Ulva biomass is a complex challenge, as each aquaculture system operates under specific environmental conditions, which directly influence the final result.

The correct classification of Ulva biomass is essential, given that about 24-32% of Ulva species are incorrectly identified in genetic databases (Fort et al., 2022), the errors being caused either by phenotypic variations influenced by environmental factors (Wolf et al., 2012) or by specific differences between the morphological and genetic traits of the species (Fort et al., 2019; Olsson et al., 2020; Toth et al., 2020; Cardoso et al., 2023). Thus, genetic improvement of seaweed can play a key role in optimizing the long-term viability, growth, and sustainability of global cultivation industries, providing significant benefits in this sector (Robinson et al., 2013).

Ulva - an alternative to fishmeal

The ratio of essential and non-essential amino acids, similar to that of soybean meal (Shuuluka et al., 2013), together with balanced protein content, comparable to that of plants (Stedt et al., 2022), are key arguments for the use of green macroalgae as alternative protein sources in fish feed. Although green seaweed has a low lipid content, it is important to note that the lipid fraction contains high levels of essential polyunsaturated fatty acids, such as linoleic acid and α-linolenic acid (Aguilera-Morales et al., 2018), which are essential for both human and fish nutrition (Zárate et al., 2017; Galindo et al., 2021).

Furthermore, saturated fatty acids like palmitic acid, which some researchers have identified as the primary component (Ortiz et al., 2006; Horincar et al., 2014), along with a low omega-6 to omega-3 fatty acid ratio, indicate that green algae may serve as a valuable food source or dietary supplement with the potential to address omega-3 deficiencies (Schmid et al., 2014; Sohrabipour, 2019). At the same time, they, are distinguished from conventional plant-based foods by their high content of minerals, such as magnesium, calcium, iron, selenium, sodium, and potassium, as well as the presence of essential vitamins, such as B12 and C, along with lipophilic vitamins, such as A and E (tocopherol) (Jacobsen et al., 2023).

Since 1984, with the first research on the use of Ulva extract in fish diets (Nakagawa et al., 1984), scientific interest in this macroalga has increased significantly. Subsequent studies investigated the effects of different species of the genus Ulva on various fish species, highlighting the potential of this resource in fish nutrition. The selection of Ulva species such as *Ulva lactuca*, *Ulva rigida*, *Ulva pertusa*, *Ulva ohnoi* and *Ulva intestinalis* was probably mainly influenced by their accessibility in the wild and their nutritional profile. Most of the studies assessed Ulva spp. coming from the wild environment (Ortiz et al., 2006; Azaza et al., 2008; Yildirim et al., 2009; Natify et al., 2009; Abdel Aziz & Ragab, 2017; Valente et al., 2016; Tapia-Paniagua et al., 2019) rather than integrated multitrophic aquaculture (IMTA) due to the low number of experiments carried out (Neori et al., 2000; Schuenhoff et al., 2003; Valente et al., 2006; Marinho et al., 2013; DM Silva et al., 2015; Shpigel et al., 2017). The partial substitution of fishmeal with green macroalgae meal has been extensively analysed, considering both the method of incorporation and the optimal inclusion levels in aquafeeds. A review of post-2015 literature reveals two primary approaches for utilizing *Ulva* spp. in fish nutrition: the direct use of raw biomass (either fresh or dried) and the integration of protein extracts obtained through advanced processing techniques, aiming to enhance digestibility and nutritional efficiency. Thus, macroalgae supplementation in the form of whole biomass (fresh or dry) ranged from 2.6% to 100% (Table 2), while integration in the form of extract ranged from 0.1% and 3% (Table 3). This variation is dependent on both the fish species and the type of Ulva spp. used in the experiments. Reported results indicated that a moderate replacement of fishmeal with Ulva can have a positive impact on the dietary intake and development of fish, due to the high nutritional value of this macroalgae. However, excessive substitution had negative effects, such as poor development and inefficient feed utilization, which reduced palatability of the diet due to the presence of anti-nutritional factors.

Scientific research has shown that the incorporation of whole macroalgae in aquaculture diets has primarily been studied in relation to growth performance, feed utilization efficiency, and body composition. In contrast, studies focusing on the use of macroalgae extracts have concentrated on evaluating their impact on health indicators, particularly immunological response and antioxidant activity, to assess potential benefits for fish health and disease resistance (Figure 1).

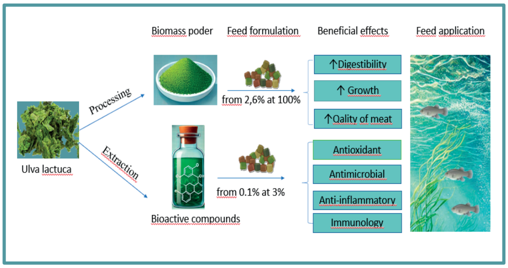

Figure 1. Overview of the use of green macroalgae in the diet of aquatic organisms and their nutritional benefits (after Gonzalez et al., 2023)

The effect of *Ulva* sp. on the fish growth

Studies focusing on the incorporation of macroalgae, either as fresh or dried biomass, in the diets of aquatic organisms has primarily focused on assessing growth performance, feed utilization efficiency, and body composition (Table 2). The integration of whole algal biomass at a 5% inclusion rate has produced inconsistent results, underscoring the need to further optimize both proportions and conditions. Thus, some research reports slower development and inefficient feed utilization for *Solea senegalensis* (Fumanal et al., 2020; Tapia-Paniagua et al., 2019), while others highlight positive growth effects on species like *Luthanus stellatus* and *Cirrhinus mrigala* (Zhu et al., 2016; Upreti et al., 2021). At the same time, Mandibana et al. (2017) identified 5% as the upper inclusion limit for Ulva macroalgae, showing that this concentration maintains both growth parameters and the health of *Argyrosomus japonicus* juveniles. Moreover, a study by Valente et al. (2016) demonstrated that including 5% Ulva spp. in the diet of *Oreochromis niloticus* led to a significant increase in carotenoid accumulation in the skin. Regarding the 10% inclusion level, studies showed improved growth and feed utilization efficiency, compared to control diets, for species like *Oreochromis niloticus* (Suryaningrum & Samsudin, 2020) or *Scatophagus argus (*Yangthong & Ruensirik, 2020). In contrast, the inclusion of *Ulva lactuca* and *Ulva rigida* in the diets of *Oreochromis niloticus* (Valente et al., 2016) and *Clarias gariepinus* (Abdel-Warith et al., 2016) is sustainable up to a 10% threshold, without negatively impacting growth parameters. Other authors (Elsharkawy et al., 2022) observed significant improvements in growth performance and feed utilization, as well as enhanced physiological responses in tilapia when replacing soybean meal with Ulva flour at a moderate 15% level. Similarly, replacing fishmeal with 14.6% *Ulva lactuca* from an Integrated Multi-Trophic Aquaculture (IMTA) system and 14.1% poultry flour resulted in performance comparable to the control diet for *Sparus aurata* (Shpigel et al., 2017).

On the other hand, higher levels of inclusion - 50% fresh *Enteromorpha* macroalgae mixed with 50% artificial feed- generated optimal performance for the herbivorous fish such as *Siganus rivulatus*. Instead, the complete replacement of artificial feed with fresh macroalgae harmed growth (Abdel Aziz & Ragab, 2017).

Castellon (2019) observed growth performance improvements in *Girella laevifrons* when supplemented with 30% Ulva, although these advances were associated with a reduced survival rate, likely due to the effects of handling or manipulation. Similarly, Younis et al. (2019) found that the inclusion of *Ulva lactuca* flour at levels of up to 20% in the diet of *Oreochromis niloticus* resulted in significant growth improvements, without any adverse effects on growth parameters or feed utilization efficiency.

Table 2. Utilization of macroalgae as whole biomass, either fresh or dried, in the fish diet

***Ulva* species**	**Fish species**	**Inclusion of *Ulva* spp.(%)**	**Effects on growth**	**Reference**
Ulva lactuca	*Girella laevifrons*	15, 30, 45	30%↑WG,low survival	(Castellón, 2019)
Ulva lactuca	*Oreochromis niloticus*	20, 40, 60	20%↑WG,SGR 60%↑carcass protein level	(Younis et al., 2019)
Ulva lactuca	*Oreochromis niloticus*	5, 15, 20, 35	15%↑WG,SGR ↓FCR 35%↑ carcass protein level	(Elsharkawy et al., 2022)
Ulva lactuca	*Sparus aurata*	2.6 & 7.8(exp1) 14.6 & 29.1(exp2)	↔WG,SGR at 14.6 ↓WG,SGR at 29.1	(Shpigel et al., 2017)
Ulva fasciata Enteromorpha	*Siganus rivulatus*	50, 100	50%↑WG,SGR↓FCR ↑lipid content in body	(Abdel Aziz & Ragab, 2017)
Ulva lactuca	*Argyrosomus japonicus*	50, 100, 150, 200 gKg^{-1}	50gKg↑WG↓SGR	(Madibana et al., 2017)
Ulva ohnoi	*Solea senegalensis*	5	5%↓WG,↔FCR	(Fumanal et al., 2020)
Ulva ohnoi	*Solea senegalensis*	5	5%↓WG,SGR↑FCR	(Tapia-Paniagua et al., 2019)
Ulva lactuca	*Luthanus stellatus*	5, 10, 15, 20	5%↑WG,SGR↓FCR,and ↓ protein and lipid content in the whole body	(Zhu et al., 2016)
Ulva meal	*Cirrhinus mrigala*	5, 10, 15	5%↑WG,SGR↓FCR	(Upreti et al., 2021)
Ulva rigida Ulva lactuca	*Oreochromis niloticus*	5, 10	5,10%↔WG,SGR,FCR 5%↑total carotenoids in skin	(Valente et al., 2016)
Ulva lactuca	*Clarias gariepinus*	10, 20, 30	10%↑WG,SGR 30%↑ protein in the muscles	(Abdel-Warith et al.2016
Ulva meal	*Oreochromis niloticus*	10, 20, 30	10%↑WG,SGR ↑body protein level	(Suryaningrum & Samsudin, 2020)
Ulva Lactuca	*Scatophagus argus*	5, 10, 15, 20, 25, 30	10%↑WG,SGR	(Yangthong & Ruensirikul,2020)

WG - weight gain; FCR - feed conversion ratio; SGR - specific growth rate; ↑ increase; ↔ no change, ↓ decrease compared to the control diet ($P < 0.05$)

Impact of *Ulva* spp. extract on antioxidant status and immune system of fish

Recent research has highlighted the potential of green macroalgae not only as a food protein source, but also as functional ingredients in diets intended for various fish species. Studies have examined the integration of green macroalgae extracts, focusing in particular on effects on oxidative status, immune response modulation, intestinal and microbiota analysis (Table 3).

Table 3. Utilization of macroalgae extracts in the fish diet

Extract seaweed	Fish species	Inclusion %	Health effects	References
Ulvan	*Oreochromis niloticus*	0.1%, 0.5% and 1%	↑ immune response	del Rocio Quezada & Fajer Avila, 2017
Polysaccharide Ulva (WPU)	*Mugil cephalus*	0.5, 10 and 15 mg kg^{-1}	WPU 10 ↑antioxidant activity ↑immune responses	Akbary & Aminikhoei, 2018
Ulvan	*Labeo rohita*	0, 25, 50 and 100 mg/kg	50 mg/kg^{-1}↑growth, ↑lysozyme activity ↑protection against F.columnare	Harikrishnan et al., 2021
Extract of Ulva/Gracilaria	*Oncorhynchus mykiss*	0.5 gkg^{-1},1.5 gkg^{-1}SPU 0.5 gkg^{-1},1.5 gkg^{-1}SPG	1.5 gkg^{-1}SPU/SPG↑growth, ↑lyzozyme activity,↑ACH50	Safavi et al., 2019
Extract of Ulva	*Chanos chanos*	0, 100, 200, 300 400 and 500 ppm	500 ppm↑growth	Nurfadillah et al., 2021
Ulva fasciata /metanol extract (UFME)	*Oreochromis niloticus*	0, 50, 100 and 150 mg kg^{-1} UFME	100 $mgkg^{-1}$↑ the length of intestinal villi,↑immunity capacity	Abo et al., 2021
Seaweed liquid extract TAM	*Oreochromis niloticus*	0.5, 1, 1.5 and 2%	2%↑growth,↑ feed utilization,↑ lysozyme activity and respiratory burst assay	Ashour et al., 2020
Seaweed mixture SME	*Pangasianodon hypophthalmus*	1, 2 and 3%	2 and 3%↑growth, ↑antioxidant status and immune biomarkers.	Abdelhamid et al., 2021
Polysaccharide Alginium(AL)	*Sparus aurata*	(3g/kg)-AL0.3 and (5g/kg) -AL0.5	↑ growth,↑innate and adaptive immune responses,↑ resistance against *Photobacterium damselae*	Güroy et al., 2022

Nevertheless, some of these studies, beside health issues, addresses also growth performance.

For instance, a study conducted on *Oreochromis niloticus* evaluated the effects of different Ulvan concentrations (from 0.1% up to 1%). The findings indicated that while supplementation did not significantly impact growth performance, it demonstrated a notable immunomodulatory potential, with its activity being sustained even after supplementation was discontinued (del Rocio Quezada-Rodriguez & Fajer-Avila, 2017). Similarly, supplementing the diet of *Labeo rohita* with 50 mg/kg of ulvan led to enhanced growth rates, increased serum lysozyme enzyme activity, and improved immune responses (Harikrishnan et al., 2021). Moreover, by modulating the expression of immuno-antioxidant genes such as GPx, CAT, and SOD, ulvan supplementation conferred protection against bacterial infection caused by *Flavobacterium columnare*.

In another study, Akbary & Aminikhoei (2018) investigated the dietary supplementation of water-soluble polysaccharides from *Ulva rigida*, particularly at the WPU 10 level, and observed a significant enhancement in lysozyme activity and phagocytic processes, contributing to an increase in final body mass. Additionally, supplementation resulted in an increase in total antioxidant content (TAC), superoxide dismutase (SOD) activity, and reduced glutathione (GSH) levels, while simultaneously leading to a considerable decrease in malondialdehyde (MDA) levels in liver tissue, indicating a reduction in oxidative stress. Mortality was significantly reduced compared to the control group, and the WPU 10 dose was found to be most effective for protecting *Mugil cephalus* against *Photobacterium damselae* infection. Another author (Safavi et al., 2019) observed that the effect of sulfated polysaccharide extract of green alga *Ulva* *intestinalis* (SPU) and red alga *Gracilariopsis persica* (SPG) produced a significant increase in growth performance, and lysozyme and serum complement activity in fish-fed 1.5% SPG and 1.5% SPU. Also, in these experimental groups, superoxide dismutase activity was lower compared to the control group.

Similarly, Abo et al. (2021) investigated the effect of supplementing the diet with methanolic extract of *Ulva fasciata* on the species *Oreochromis niloticus*, finding that a concentration of 100 mg/kg resulted in significant increases in final weight. The trial emphasized significant improvements in the length of intestinal villi, which was considerably increased in all segments of the intestine. The enzymatic activity of SOD and CAT was also significantly higher ($p < 0.05$). In addition, there was an increase in lysozyme activity and phagocytic activity, indicating an improvement in immune mechanisms. Nurfadillah et al. (2021) also observed that the diet containing ethanolic extract at a concentration of 500 ppm resulted in the best growth performance for *Chanos chanos*. Other studies demonstrated that adding up to 2% of the commercial seaweed supplement TrueAlgaeMax (TAM) to the diet of *Oreochromis niloticus* optimizes growth, feed efficiency and nonspecific immunity against *Aeromonas hydrophila* infections (Ashour et al., 2020), while adding an extract from a mixture of seaweed in proportions of 2-3% it improves the antioxidant status, highlighting the protective effect on the liver of fish, and supports both innate immunity and growth performance (Abdelhamid et al., 2021).

Güroy et al. (2022) pointed out the potential use of Algimun® - a mixture of sulfated marine polysaccharides in the *Sparus aurata* diet, demonstrating that supplementation with this additive significantly improves growth performance, reduces the rate of food conversion, and stimulates both innate and adaptive immune responses. It was also found to increase fish resistance and survival from *Photobacterium damselae*.

Strategies for macroalgae integration in fish nutrition

The marine macroalgae industry is well consolidated and contributes about 30% to global aquaculture production. Annually, it generates a volume of about 30 million tons, with an estimated value of over 6 billion dollars. The main producing countries are China and Indonesia, which contribute about 90% of total production (Hua et al., 2019). In Europe, the macroalgae industry continues to be dominated by harvesting from natural ecosystems, which provides 68% of the total production units. However, macroalgae aquaculture, carried out in both terrestrial and marine systems, is in full development in several European countries, reaching to cover 32% of the production capacity. Norway stands out as the main producer of marine algae biomass in Europe (Araújo et al., 2021). Ulva spp. are not among the most intensively cultivated species in aquaculture. The main producers of green algae *Ulva* spp. are South Africa, with a production of 3,175 tons in 2020, and China, with a volume of 200 tons in the same year (Hofmann et al., 2024). In Europe, production data was not fully reported to the FAO, only information provided by Portugal and Spain is available. The economic impact of using this macroalgae in the fish diet remains poorly documented.

Shpigel et al. (2017) were the first to estimate the economic benefits associated with the use of Ulva in an integrated multi-trophic aquaculture system (IMTA), highlighting the impact on feed costs, fish production, and operational expenditure. Given that fish feed may account for more than 60% of total costs in intensive aquaculture, a reduction of around 10% of these expenses is of significant economic importance.

Challenges associated with NSPs in macroalgae

Due to their rich nutritional composition, macroalgae are regarded as a promising ingredient for aquafeeds. However, their widespread utilization is constrained by the presence of antinutritional factors, particularly non-starch polysaccharides (NSPs) such as cellulose, galactans, xylans, and hemicellulose, which can negatively impact digestibility and nutrient absorption. When included in high proportions, these compounds reduce feed palatability, hinder the efficient utilization of nutrients, and ultimately impair growth performance (Abdel-Warith et al., 2016;

Moutinho et al., 2018; Tapia-Paniagua et al., 2019). In this context, the use of enzymes as feed additives for fish was investigated to evaluate their potential effects as a means of improving the efficiency of the feed and, implicitly, the digestibility of macroalgae proteins (Castillo & Gatlin, 2015; Xie et al., 2019). All diets have been accepted by fish, and those with enzymes have shown beneficial effects on growth and digestion, without significant differences from the control diet. This suggests that enzymes could reduce the disadvantages of macroalgae-based diets. Similarly, the study conducted by El-Mousalamy et al. (2022) investigated the feeding of *Oreochromis niloticus* to evaluate the effects of supplementing *Ulva lactuca* -based diets with exogenous enzymes, including a monoenzymatic and multienzymatic complex (MEM), as well as yeast. A fishmeal-based (FM) diet was used as a positive control. The results indicated that the diet supplemented with the multi enzymatic complex (MEM) achieved the highest growth parameter values, with no significant differences between this treatment and the control dietThe feed conversion coefficient (FCR) values were significantly lower in fish fed on the fish meal (FM) diet and on diets containing Ulva supplemented with enzymes or yeast. The increased feed conversion efficiency and palatability of the diet can be attributed to the more effective release of nutrients from plant diets, due to the degradation of antinutritional factors (ANF). These processes favored both the development of protein digestion and more efficient absorption of amino acids (Maryam et al., 2024)

In addition to the advantages of enzyme supplementation, the use of probiotics as additives in the diet presents promising prospects, providing multiple benefits to the hosts. They contribute to the production of digestive enzymes, stimulating the intestinal microflora and thus enhancing nutrient intake and intensifying fish metabolism (Zamini et al., 2014; Adeoye et al., 2016). This aspect is also highlighted in the study conducted by Amer et al. (2020), which evaluated the impact of using fermented lactic algae (FER) and exogenous enzyme blends supplemented with Natuzyme®, administered in combination with L-carnitine (LC) and/or probiotics (PRO) in the diet of *Oreochromis niloticus*. Additionally, the research conducted by Tharaka et al. (2020) analyzed the effects of supplementing the diet of *Paralichthys olivaceus* with algal clay powder, derived from *Ulva lactuca* and *Solieria chordalis*, integrated into exfoliated micronized montmorillonite (ACP). The results indicated that a fishmeal-deficient diet supplemented with 0.2% algal clay powder had beneficial effects on growth parameters and feed utilization efficiency. These improvements were attributed to the presence of bioactive compounds in the algae and the optimization of intestinal morphology due to montmorillonite (Nur et al., 2020; Karimi et al., 2020)

Another similar study conducted by Gunathilaka et al. (2021) investigated the effect of dietary supplementation with marine algae extracts (*Ulva* spp. and *Solieria* spp.), both in the presence and absence of organic acids, on the species *Paralichthys olivaceus*. The results indicated that dietary supplementation had a beneficial impact on intestinal morphology and digestive enzyme activity. Increased activity of digestive enzymes has also been reported in other studies conducted on various fish species such as *Sciaenops ocellatus* and *Oreochromis niloticus* fed diets enriched with organic acids (Castillo et al., 2014; Addam et al., 2019).

Antinutrients in macroalgae: implications for fish nutrition

The bioactive compounds in macroalgae are essential for maintaining health, helping to increase nutrient absorption, creating gut microbiota, and supporting immune function. Although they bring numerous nutritional benefits, it is important to consider the presence of antinutrients in their biochemical composition. Among the antinutrients found in macroalgae, the most common are: tannins, phytates, oxalates, saponins, lectins, and alkaloids (Francis et al., 2001; Gemede, 2014). These natural compounds can affect the absorption and use of nutrients, thus having a significant impact on fish health. To mitigate the adverse effects of nutrients, various processing methods can be used, such as fermentation and thermal and enzymatic treatments. These techniques can reduce the levels of antinutrients and increase the nutritional values of macroalgae. On the other hand, macroalgae extracts are a promising alternative that offers higher concentrations of specific bioactive compounds thus providing potential additional benefits.

The thermal processing of macroalgae can be carried out for various purposes, including inactivation of associated microorganisms, thus facilitating their use in human nutrition. Also, this process can help create the nutritional value of macroalgae, making them more suitable as additives in the feed of aquatic organisms. The effect of thermal processing on the macroalgae *Ulva hanoi* was investigated in a 90-day feeding study conducted on *Solea senegalensis* (Vizcaino et al., 2019). In this study, the diet enriched with 5% Ulva was processed through a four-section extruder, applying a progressive thermal profile: 100°C at the beginning, followed by 95°C, 90°C, and finally 85°C at the exit. Experiments have demonstrated good food acceptability without a significant impact on food consumption. However, the temperature applied during extrusion was not sufficient to fully inactivate the protease inhibitors present in the macroalgae. Nevertheless, analysis of the ultra-structural morphology of the intestinal mucosa showed an increase in the absorption surface after 45 days of administration, an effect that was not maintained until the end of the experimental period**.**

Similarly, other authors (Fernandes et al., 2022) evaluated the impact of innovative treatments on the composition and structure of the macroalga *Ulva rigida*, aiming to integrate it into the diets of aquatic organisms, using *Dicentrarchus labrax* as an experimental model. In this study, six experimental variants were tested, in which 5% of the feed ingredients were replaced with treated *Ulva rigida* macroalgae using various methods: alkaline, autoclave, ultrasound, microwave, liquid fermentation with microwave (SSF), and solid fermentation followed by sequential hydrolysis (SSF-SH). Of these, SSF-SH caused the greatest degradation of cellulose and hemicellulose, as well as the release of the highest amounts of reducing sugars. Although fish have accepted all experimental diets, *Ulva rigida* supplementation, regardless of treatment, reduced voluntary food consumption and significantly affected the growth performance compared to the positive control diet. The only exception was represented by the variant treated by SSF, which sustained similar growth to that seen in the positive control group.

In contrast, a study conducted by Magnoni et al. (2017) on the species *Sparus aurata* examined the effects of supplementing the diet with 5% thermal-treated marine algae *Gracilaria vermiculophylla* and *Ulva lactuca*, without highlighting any significant differences in fish growth performance. The assessment of extraction technologies is essential for the sustainable exploitation of bioactive compounds from *Ulva* spp. and other plants. The optimal choice of solvent, time and temperature influences the yield and activity of compounds (Pappou et al., 2022). New extraction technologies, although more efficient and environmentally friendly, present both advantages and challenges to traditional methods, which are mostly manual, require long periods of operation, are consuming toxic and environmentally harmful solvents (Usman et al., 2022). Among the innovative extraction techniques, several methods have gained attention for their efficiency, selectivity, and environmental sustainability.

Enzyme-assisted extraction (EAE) is particularly effective for obtaining proteins and hydrolysates from macroalgae, with the choice of enzyme depending on the desired final product. Although less widely adopted, this technique is recognized for its high extraction yields, compound selectivity, and low energy consumption, while operating under mild and non-toxic conditions (Hardouin et al., 2016; Vasquez et al., 2019).

Ultrasound-Assisted Extraction (UAE) utilizes ultrasound waves with frequencies ranging from 20 kHz to 10 MHz, offering a rapid and straightforward extraction process with low solvent consumption, minimal environmental impact, and high economic efficiency. UAE is particularly suitable for extracting thermolabile bioactive compounds, ensuring their integrity for further processing. This technique provides high yields and excellent efficiency in preserving the bioactivity of extracted compounds (Essa et al., 2018; Rashad et al., 2023).

Supercritical Fluid Extraction (SFE) is an eco-friendly technique known for its high efficiency and rapid extraction rates, using supercritical CO_2 as a solvent. One of the key advantages of SC-CO_2 is its ability to exhibit both gas and liquid properties at the critical point, allowing for effective interaction with target compounds during extraction (Fabrowska et al., 2016). SFE offers mild critical conditions, solvent-free final products, and the selective extraction of desired substances. However, its disadvantages include high equipment costs, complex cleaning procedures, the need for high-pressure operation, and limited solubility of certain fat-soluble compounds, requiring optimization for efficient extraction (Martins et al., 2023).

Microwave-Assisted Extraction (MAE) ensures the rapid and selective extraction of bioactive compounds with low energy and solvent consumption, while also generating minimal waste. This technique is widely applicable and more cost-effective than supercritical fluid extraction, making it a promising method for the natural extracts industry (Mirzadeh et al., 2020; Andre et al., 2023). However, MAE requires additional procedures for the separation of residues of bioactive compounds and can cause damage to their structure due to high temperatures (Martins et al., 2023).

Pressure liquid extraction (PLE) is an advanced, sustainable and efficient development, that provides high yield and fast extraction process (Quitério et al., 2022). This allows the use of various solvents including organic, alkaline, ionic, or hot water liquids, known as hot water pressure extraction (PHWE) or subcritical water extraction (SWE). However, it produces a non-selective extraction of compounds, which can be compensated by the use of adsorbents. Although the initial cost of the equipment is high, it is counterbalanced by the low consumption of solvents and small quantities (Perez-Vazquez et al., 2023).

In conclusion, trends in the development of emerging technologies will continue to grow as sustainable alternatives to address environmental challenges, optimizing extraction methods to reduce energy and resource consumption. Increasing the efficiency of the extraction process can be achieved by combining different technologies, and promoting innovative and promising solutions.

CONCLUSIONS

This evaluation highlighted several insufficiently explored issues that limit the optimal integration of macroalgae as a commercial ingredient in feed for aquaculture animals.

Thus, macroalgal ingredients can partially or totally replace fish meal, with substitution levels ranging from 0% to 100%. The maximum degree of replacement depends on the species of macroalgae used, the feeding habits of fish, and inclusion into diet method.

In conclusion, green macroalgae are a viable option for aquaculture due to the many benefits it offers. In addition to being a sustainable source of nutrients, they contain bioactive compounds that have beneficial effects on the health and growth of farmed fish. The use of green macroalgae in aquaculture feed can help to reduce dependence on conventional ingredients, thereby reducing pressure on wild fish stocks and terrestrial resources. However, further research is therefore needed to assess and optimize their effectiveness, thereby facilitating sustainable application in aquatic production systems.

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