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Prospects of dietary seaweeds and their bioactive compounds in sustainable poultry production systems: A symphony of good things?

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Modern poultry production systems face numerous economic, environmental, and social sustainability challenges that threaten their viability and acceptability as a major source of animal protein. As scientists and producers scramble to find cost-effective and socially acceptable solutions to these challenges, the dietary use of marine macroalgae (seaweeds) could be an ingenious option. Indeed, the incredible array of nutritive and bioactive compounds present in these macroscopic marine organisms can be exploited as part of sustainable poultry production systems of the future. Incorporating seaweeds in poultry diets could enhance feed utilization efficiency, growth performance, bird health, meat stability and quality, and consumer and environmental health. Theoretically, these benefits are mediated through the putative antiviral, antibacterial, antifungal, antioxidant, anticarcinogenic, anti-inflammatory, anti-allergic, antithrombotic, neuroprotective, hypocholesterolemic, and hypoglycemic properties of seaweed bioactive compounds. Despite this huge potential, exploitation of seaweed for poultry production appears to be constrained by a variety of factors such as high fibre, phenolics, and ash content. In addition, conflicting findings are often reported when seaweeds or their extracts are used in poultry feeding trials. Therefore, the purpose of this review paper is to collate information on the production, phytochemical components, and nutritive value of different seaweed species. It provides an overview of *in vivo* effects of dietary seaweeds as measured by nutrient utilization efficiency, growth performance, and product quality and stability in poultry. The utility of dietary seaweeds in sustainable poultry production systems is explored, while gaps that require further research are highlighted. Finally, opportunities that exist for enhancing the utility of seaweeds as a vehicle for sustainable production of functional poultry products for better global food and nutrition security are presented.

KEYWORDS

antibiotic growth promoters, bioactive compounds, meat quality, poultry nutrition, seaweeds, sustainability

Introduction

The important role that poultry products play in the food and nutrition security of millions of households globally remains unequivocal. This is supported by poultry production statistics that show rapid, continuous gains worldwide. For example, in 2017, chicken meat contributed 37% of total meat produced globally (FAOSTAT, 2020). Poultry products are especially important for human nutrition in developing nations because of their affordability, higher availability, and limited religious restrictions (FAO, 2013). The race to meet a rapidly increasing demand for poultry products has seen the emergency of large-scale, industrialized poultry farms that are heavily reliant on chemotherapeutics (Lee et al., 2012) while paying little attention to bird welfare (Karcher and Mench, 2018), product quality or environmental stewardship (Amato et al., 2020). There is a general tendency for poultry producers to focus on maximizing production at any cost, an approach that is environmentally, socially, and economically unsustainable, given that most resources on earth are finite. The net effect of this approach has been the widespread erosion of societal confidence in the ability and desire of the industry to meet its obligations to society (Hafez and Attia, 2020). Recent changes towards alternative organic poultry production systems (Jeni et al., 2021) are an attempt to restore this confidence and secure the social license needed to continue operations. To compound matters, most of the land-based feed resources used in the formulation of poultry diets, such as maize grain and soybeans, are also good enough for direct human consumption thus inflating their demand and market prices on the world market (Masenya et al., 2021). In addition, cultivation of these feed resources directly generates greenhouse gas emissions (Theurl et al., 2020) while the expansion of arable lands often leads to deforestation that decimates vital carbon sinks (Theurl et al., 2020). This makes current poultry production systems environmentally unsustainable. Yet another challenge relates to the use of prophylactic antibiotics in modern intensive poultry production systems to prevent infectious and stress-induced diseases and enhance feed utilization efficiency (Engberg et al., 2000). This practice has been shown to promote antibiotic resistance and accumulation of antibiotic residues in poultry products, outcomes that have negative implications on human health (Cervantes, 2015). Attempts to mitigate the sustainability challenges in poultry production have taken many forms, including the dietary incorporation of seaweeds (Nhlane et al., 2020; Matshogo et al., 2021; Stokvis et al., 2022). These marine macroalgae can be produced sustainably in oceans with no requirement for fresh water, fertilizers, or land (Duarte et al., 2017). They play a role in climate change adaptation and mitigation through carbon sequestration as part of the blue carbon economy (Yong et al., 2022). These marine organisms can be used as safe and environmentally friendly feed ingredients. Their nutrients and bioactive compounds have been reported to modulate the immune system, improve nutrient utilization efficiency and growth performance, enhance product quality and stability, and prevent disease outbreaks in poultry (Matshogo et al., 2021; Stokvis et al., 2022). These desirable effects are thought to be mediated through antibacterial, antifungal, antiviral, vermifuges, neuroprotective, antitumoral, anti-inflammatory, anti-allergic, antithrombotic, hypocholesterolemic, and hypoglycemic properties of seaweed bioactive compounds (Matshogo et al., 2021). Seaweeds are also rich in n-3 long chain polyunsaturated fatty acids (LC-PUFA), thus products from birds reared on seaweed-containing diets are likely to supply physiologically effective doses of beneficial LC-PUFA to consumers. Despite these potential benefits, the use of seaweeds in poultry diets is not as prevalent as expected due to several challenges, ranging from low availability, poor accessibility, high cost, low digestibility (Matshogo et al., 2021; Costa et al., 2022), lack of regulatory framework specific to their use as nutraceuticals for poultry, and lack of information on how best to incorporate them in practical poultry diets. This review provides an overview of *in vivo* effects of dietary seaweeds as measured by nutrient utilization efficiency, growth performance, and product quality and stability in poultry. The paper also explores the consensus and contradictions that exist in literature regarding the utility of dietary seaweeds in sustainable poultry production systems while highlighting the gaps that require further research.

Towards sustainable poultry production

Poultry production and consumption statistics

Like it has been for millennia, poultry products continue to serve as affordable sources of animal protein for people, especially in low-income countries. It is, therefore, not surprising that the poultry industry is currently the largest and fastest growing animal agriculture sub-sector in developing countries. Globally, poultry meat and eggs are one of the most consumed animal products and their demand is expected to continue to rise owing to the ever-growing human population, urbanization, and increasing income (Øverland et al., 2019). Indeed, the Food and Agriculture Organisation reported a global population of 23 billion poultry birds in 2016, translating to at least three birds per person (FAOSTAT, 2016). About 73 million tons of eggs and nearly 100 million tons of poultry meat are produced globally (Mottet and Tempio, 2017). Approximately 92% of poultry meat comes from high-input large-scale broiler systems with layers only contributing 6% of the total (Mottet and Tempio, 2017). The backyard systems are said to contribute around 2% of poultry meat and 8% of eggs worldwide (Mottet and Tempio, 2017). However, it should be noted that there is a

huge variation in the consumption of poultry meat and eggs among countries, with much lower figures likely in poorer countries. This suggests that sustained efforts are required to ensure that households in low-income countries have access to affordable and high-quality poultry products. This requires the development of sustainable and efficient production systems that would ensure that the poultry industry continues to contribute towards food and nutrition security across diverse cultures, religions, and ethnic groups. The high nutrient density of poultry products together with the birds' fast growth rates, high feed conversion efficiency, and short production cycles should be exploited as favorable attributes to alleviate protein-energy malnutrition and eradicate food insecurity in hunger-stricken countries.

Sustainability challenges facing poultry production

Even though the poultry industry is the fastest-growing agricultural subsector, production is projected to increase at a slower rate than in previous decades owing to high production costs driven by exorbitant feeding costs. Nkukwana (2018) alluded that feed costs, which constitutes about 75% of total production costs, hamper profit margins in animal agro businesses. This is commonly attributed to the volatile changes in maize and soybean prices. These two ingredients have direct food value for humans and their demand continues to increase in the food, feed, and biofuel sectors, which consequently leads to higher market prices. Accordingly, many scholarly reports have indicated that the over-reliance on these ingredients for poultry feed formulation is economically, socially, and environmentally unsustainable for large-scale poultry intensification (Marareni and Mnisi, 2020). Moreover, cultivation of maize and soybeans requires large hectares of arable land, large volumes of water, fertilizers, pesticides, fuel, and machinery, among others (Marareni and Mnisi, 2020). From an environmental standpoint, the cultivation of maize and soybeans results in deforestation, soil compaction and erosion, eutrophication, pollution, and high atmospheric carbon footprint (Castanheira and Freire, 2013), which is undesirable in the face of climate change. In addition, to prevent stress-induced disease outbreaks and enhance feed utilization efficiency in modern intensive poultry production systems, in-feed prophylactic antibiotics have been the strategy of choice (Engberg et al., 2000). However, reliance on in-feed antibiotics also increases production costs because they are relatively expensive (Thema et al., 2019). Moreover, there is on-going public concern that using antibiotics in this manner contributes to antibiotic resistance with negative implications on human health (Cervantes, 2015). Antibiotic residues in poultry products are also a major concern as they are reported to cause negative health outcomes in consumers (Thema et al., 2019).

Sustainable poultry production: What role for seaweeds?

In response to climate change and population growth, there has been increasing global interest in the use of seaweeds to promote sustainable animal production systems. Seaweeds are a valuable natural resource that serves as a remarkable source of functional constituents with promising applications in food and feed for humans and animals, respectively. They are categorized into three colour pigment groups: red including about 7000 species of *Rhodophyta*; brown including about 2000 species of *Phaeophycea*; and green with about 1000 species of *Chlorophyta* (Ganesan et al., 2019). Various seaweed species have attracted extensive research attention from biomedicine to agri-food industries as putative sources of multiple biologically active compounds such as proteins, glycoprotein, minerals, vitamins, essential fatty acids, fucoidan, carotenoids, peptides, dietary fibers, oxylipins, violaxanthin, steroids, zeaxanthin, phlorotannins, lutein, fucoxanthin, and laminarin (Venkatesan et al., 2019). Due to the presence of these bioactive compounds, there has been growing interest from researchers to use seaweeds for various applications in medicine, cosmetics, biofuel, and fertilizer-manufacturing industries (Poza et al., 2022). Indeed, these bioactive compounds have functional benefits with antioxidant, antimicrobial, hypoglycemic, antiradiation, immunomodulatory, anti-inflammatory, anticancer, growth-stimulating, meat-boosting, and health-promoting properties (Wang et al., 2019). Apart from their nutraceutical properties, seaweeds are sustainable natural bioresources that do not compete with terrestrial plants for arable land, fresh water, pesticides, fertilizers, and insecticides to grow, and yet they have high productivity (Balina et al., 2017). Seaweeds acquire nutrients directly from the sea. All these desirable characteristics suggests that utilizing seaweeds as a functional feed ingredient in poultry nutrition could reduce feed-food competitions and thus deliver efficient, sustainable, and profitable poultry production systems. The use of seaweeds as poultry feed ingredients will also ensure that consumers have indirect access to bioactive compounds through the consumption of high-quality, functional poultry products. This strategy requires the optimization of seaweed production, harvesting, processing, and distribution systems to ensure that the product is readily available at low cost.

Seaweeds: Growth habit, production, harvesting, and processing

Growth habitat and production of seaweeds

Seaweeds are botanically classified as macroalgae and can grow in the shallow waters at the edge of the ocean. Globally, there are several types of seaweeds that can be found floating and

submerged in the intertidal zone and ocean tropical waters (Hayashi et al., 2010). In their natural environment, seaweeds grow on rocks, stones, pebbles, and dead corals while some exist as epiphytes (Bhagyaraj and Kunchithapatham, 2016). Given the rapidly increasing demand for seaweeds that is driven by the search for natural bioactive products (Harb and Chow, 2022) for use in pharmaceutical and feed/food industries, it is important to sustainably intensify the production of seaweeds. In 2015, an estimated 196 570 tons of seaweeds were produced worldwide, however, there was a 43% reduction in production between 2015 and 2018 due to climate-induced outbreaks of pests and diseases (Sánchez-Velásquez et al., 2021). In 2019, total algae production was recorded at about 36 million t (FAO, 2021), of which 50% was produced from seaweed aquaculture systems.

Cultivation of seaweeds is one of the most important global food/feed production activities because it also offers opportunities for mitigation and adaptation to climate change (Duarte et al., 2017), in addition to providing valuable natural bioactive compounds. However, global seaweed production is experiencing relatively low growth rates due to slow growth of tropical seaweeds species (FAO, 2020) and unprecedented pest and disease outbreaks in cultivated seaweed systems (Ward et al., 2020). For example, in the Philippines, outbreaks of 'ice–ice' disease and epiphytic pests have reduced seaweeds yields (Kambey et al., 2020). Globally, seaweed diseases and pests have become increasingly common in the past decade, threatening the future of the seaweed industry, especially of the higher value *Kappaphycus* sp. (Largo et al., 2020). The main method of cultivation is the bottom monoline technique, which is applied in shallow waters in the nearshore/intertidal zone, allowing the lines to be exposed during the spring low tide. Other cultivation methods such as the raft, broadcasting, and net methods, have not been evaluated for economic feasibility to allow their use in commercial farming (Kimathi et al., 2018). Cultivated and naturally occurring seaweeds, including beach-cast ones, are the two major sources of these macroalgae. There is currently limited research on the differences between cultivated and wild seaweeds, however, some studies have reported that their nutritional composition, physical make-up, and subsequent utilization depend on the harvesting site, water temperature or pH, salinity, concentration of heavy metals, light intensity, as well as the employed processing method (Chizhov et al., 1998; Kadam et al., 2015; Nhlane et al., 2020). Nonetheless, frequent collection and utilization of seaweed on beaches also creates an attractive environment for tourism while providing the feed industry with a low-cost source of beneficial bioactive compounds.

Harvesting of seaweeds

The cleaning process of beaches is part of the harvest activities of beach-cast seaweeds, which is done in accordance with the rules and regulations that govern treatment of organic waste in most jurisdictions. However, this waste biomass can be reused to produce agar (*Gelidium*), as fertilizer for crops (Lorbeer et al., 2013), or as a feed ingredient in various food animal production systems, including poultry. Unfortunately, harvesting beach-cast seaweeds has the unintended consequence of removing between 100 and 400 m^3 of sand per harvesting season, thus increasing erosion and changing the topography of beaches (Hyndes et al., 2021). In South Africa, commercially harvested beach-cast seaweed is mainly used for human consumption and in nutraceutical, cosmetic, and fucoidan-processing industries (Poza et al., 2022). For seaweeds that are not beach-cast, harvesting traditionally involves cutting fronds during the low tide using boats. The whole "head" is then pulled aboard, leaving the stipe and holdfast to die. Recovery of the biomass then requires the growth of new sporophytes occur. Ashore, the fronds are then cut off and the primary blade discarded. Another type of harvesting method that is based on experiments reported by Levitt et al. (2002) has been proposed. It involves excising only the distal parts of the secondary blades and leaving at least 20 – 30 cm of their bases (with the basal meristems intact) attached to the primary blade, allowing fronds to be harvested again within a short period of time. This non-lethal harvesting approach by Levitt et al. (2002) is said to allow higher biomass yields over time. However, given that frond regrowth rates decline as the sporophytes age, it may be necessary to carry out periodic lethal harvests to allow new plants to emerge and contribute to biomass yield.

Chemical composition of seaweeds

While seaweeds are a rich source of nutrients and bioactive compounds, including carotenoids, proteins, peptides, vitamins, minerals, oxylipins, phlorotannins, steroids, minerals, essential fatty acids, dietary fibers, polysaccharides, and sulphated polysaccharides (Venkatesan et al., 2019), their chemical composition varies greatly. Indeed, the concentration and profile of chemical components of seaweeds is influenced by many factors including species, geographical location, drying process, harvesting, humidity, season, and temperature (Garcia et al., 2016). Species variation in type and concentration of bioactive compounds is so wide that certain species even contain toxic rather than beneficial compounds. This information is crucial as such compounds can limit the utilization of seaweed species as feed for animals. For example, *Caulerpa saxifolia* contains sesquiterpene caulerpyne that blocks the mitotic cycle of sea urchin embryos and inhibits stimulation of mitogen-activated protein kinase (Mozzachiodi et al., 2001). The likelihood of such compounds exerting their negative effects in food animals such as chickens is high and should be carefully investigated prior to incorporation in poultry diets. Huge within-genus variations in terms of chemical composition have

been demonstrated (Lares et al., 2002) as shown in Tables 1, 2. Chemical composition of seaweeds has also been demonstrated to vary with environmental changes as modulated by seasons. Indeed, a study conducted by Marinho-Soriano et al. (2006) reported a positive correlation between carbohydrates content and temperature in the red seaweed, *Gracilaria caudate*. Similarly, Hu (2004) revealed that high light intensity increases the production of polysaccharides in seaweeds. In a study by Manns et al. (2017) sugar levels were higher in summer compared to winter in the brown seaweeds, *Laminaria digitata* and *Saccharina latissima*. The growth stage of seaweed species can also affect the biosynthesis, presence/absence, and potential bioaccumulation of various chemical constituents (Zou et al., 2018). However, limited understanding of the mechanisms through which environmental parameters influence the levels of nutrients and bioactive compounds continue to hinder the full exploitation of seaweeds as animal feed ingredients (Cassani et al., 2020).

The concentration and bioactivity of beneficial compounds in seaweeds can also be affected by processing methods. The most common seaweed processing method is moisture removal through sun-drying (Carrillo et al., 1992), oven-drying (Hamdy and Dawes, 1988), and freeze-drying (Mabeau et al., 1992). These methods can drastically increase the shelf-life of seaweeds. Drying is also a preparatory step in the extraction of important chemical constituents from seaweeds. However, drying can affect the quality, color, aroma, as well as their and nutrient and phytochemical concentration (Chan et al., 1997). The quality of seaweed can be reduced if heat-labile beneficial compounds are lost during the drying process. For example, phenolic compounds (capable of acting as antioxidants) are often depleted upon drying resulting in reduction in antioxidant value of dried products (Badmus et al., 2019). For example, according to Mabeau and Fleurence (1993) drying at high temperatures greatly alters the vitamin C content in brown seaweed. In addition, the bioavailability of molecules such as amino acids, proteins, lipids, fatty acids, and secondary compounds in seaweeds may also be negatively affected by drying process (Silva et al., 2019).

The species-induced variation in proximate composition (on a dry matter basis) of seaweeds is presented in Table 1. For example, within the red seaweed group, neutral detergent fibre (NDF) content can be as high as 43.1% in *Porphyra* sp. and as low as 27.2% in *Asparagopsis armata*, while within green seaweeds (*Ulva* sp.) a much narrower range (22.8 to 26.2%) has been reported (Table 1). In brown seaweeds, NDF content can be as high as 22.0% in *Ascophyllum nodosum* and as low as 16.6% in *Laminaria* sp. Wide species-depended variations in ash content are evident in *Ulva* sp. (7.7 – 23%) and brown seaweeds (22 – 32.9%) but not in red seaweeds (6.5 – 10%). There is limited species variation in lipid (ether extract) content of seaweeds, which is generally below 1% except in *A. nodosum* where as high as 3.9% ether extracts were recorded (Table 1). Species differences in terms of crude protein content are also evident, especially within the red seaweed group, where it can be as high as 38.1% in *Porphyra* sp. and as low as 17.8% in *A. taxiformis*. In brown seaweeds, crude protein content varies widely, ranging from 6 (*A. nodosum*) – 16.6% (*Laminaria* sp.). Differences in the crude protein content of the seaweeds can be caused by the drying and/or processing methods used after harvesting. The protein value also differs according to the value of the nitrogen-to-protein conversion factor used. The average value of the nitrogen-to-protein conversion factor is 5.13 for green seaweed, 5.38 for brown seaweed and 4.92 for red seaweed (Lourenço et al., 2002). In addition, seaweed is a significant source of some water-soluble and lipid-soluble vitamins. Water-soluble vitamins in seaweed are represented by vitamin C and vitamins of the B group, especially B_1, B_2 and B_{12}. In a systematic review of 92 seaweed species, vitamin C content was found to be 0.773 mg/g DM of seaweed with a 90th percentile of 2.06 mg/g DM (Nielsen et al., 2021).

TABLE 1 Species-induced variation in proximate composition (% DM) of seaweeds[1].

Seaweed types	Proximate components				
	NDF	ADF	Ash	CP	EE
Red seaweed					
Porphyra sp.	43.1	6.6	6.5 - 8.7	24.6 - 38.1	0.3 - 0.5
Asparagopsis taxiformis	36.9	11.6	–	17.8	0.4
Asparagopsis armata	27.2	10.9	10.0	18.3	0.32
Green seaweed					
Ulva sp.	22.8 - 26.2	7.6 - 8.7	7.7 - 23.2	15.3 - 18.5	1.2
Brown seaweed					
Ascophyllum nodosum	20.9 - 22.0	13.1	22.0 - 22.5	6.0 - 8.3	3.9
Macrocystis sp.	19.9	12.6	32.9	10.1	0.6
Laminaria sp.	16.6	–	29.9 - 31.5	9.8 - 16.6	0.8

Proximate components: NDF, neutral detergent fiber, ADF, acid detergent fiber, CP, crude protein, EE, ether extract.
[1]Sources: Farley (2012); Abudabos et al. (2013); Hind et al. (2014); Machado et al. (2016); Marino et al. (2016); Aminina et al. (2020); Min et al. (2021).

TABLE 2 Species-induced variation in mineral composition of seaweeds[1].

Seaweed type	Calcium (%)	Phosphorus (%)	Magnesium (%)	Sodium (%)	Iron (mg/kg)	Manganese (mg/kg)	Copper (mg/kg)	Zinc (mg/kg)
Red seaweed								
Porphyra sp.	4.4	3.8	4.9	4.1	2.2	–	0.51	0.15
Asparagopsis taxiformis	3.8	0.2	0.8	6.6	6.2	0.1	0.24	0.87
Asparagopsis armata	4.47	0.27	1.38	9.36	1.24	0.10	–	0.07
Green seaweed								
Ulva sp.	2.9	0.27	1.7	2.0 - 3.3	1.24	0.10	7.07	0.05
Brown seaweed								
Ascophyllum nodosum	1.0 - 30	0.1 - 0.2	0.5 - 1.09	2.4 - 4.0	134.0	10.50	4.0 – 15	35.10
Macrocystis sp.	14.1	2.5	39.2	36.5	117.0	11.0	2.0	12.0
Laminaria sp.	25.3	–	5.5	25.3	233.2	6.2	14.9	11.7

[1]Source: Anderson et al. (2006); Holdt and Kraan (2011); Farley (2012); Belanche et al. (2016); Nunes et al. (2018); Roque et al. (2019); Min et al. (2021).

The species-induced variation in mineral composition of seaweeds is represented in Table 2. Within the red seaweed group, Ca content can be high as 4.47% in *A. armata* and as low as 3.8% in *A. taxiformis*. However, in brown seaweed, Ca content can be high as 25.3% in *Laminaria* sp., but as low as 1.0% in *A. nodosum*. Most seaweed species presented in Table 2 have P levels ranging from 0.1 to 0.27% while *Porphyra* sp (3.8%) and *Macrocystis* sp. (2.7%) registered very high P levels. Within red seaweed species, Mg content can be high as 4.9% in *Porphyra* sp. And as low as 0.8% in *A. taxiformis*. However, in brown seaweeds, the variation in Mg content is much larger ranging from 0.5% in *Ascophyllum nodosum* to 39.2% in *Macrocystis* sp. Species-dependent variation in Na content is much lower in red seaweeds (4.1 – 9.36%) compared to brown seaweeds where it ranges from 2.4% in *A. nodosum* to as high as 36.5% in *Macrocystis* sp. In general, brown seaweeds species seem to have higher levels of Fe, Mn, Cu, and Zn compared to red seaweeds (Table 2). Species differences in mineral composition of seaweeds is expected since the processes of absorption, utilization and bioaccumulation of minerals are genetically controlled.

Bioactive compounds in seaweed and their potential benefits in poultry

The increasing interest in seaweeds as functional feed ingredients in poultry production is driven by the myriad of primary and secondary plant compounds (Table 3) that have both nutritional and pharmaceutical properties (Ummat et al., 2021). These bioactive chemicals are naturally occurring essential and non-essential compounds that have been demonstrated to alter human and animal health (Michalak

and Mahrose, 2020). The listed seaweed bioactive compounds have been demonstrated to possess antioxidant, antimicrobial, immunomodulatory, antiviral, antitumor, and antibacterial properties (Ummat et al., 2021). These makes these compounds essential in optimizing gut environment, inhibiting oxidative stress and inflammation, enhancing immunity, and improving growth performance in animals. Indeed, improvement on feed intake, average daily gain, feed conversion ratio; reduction on meat fat pads; increased egg and shell weights; and reduced egg and serum cholesterol and total lipids have been attributed to these bioactive compounds (Catarino et al., 2020; Michalak et al., 2022).

Carotenoids

Carotenoids are pigments that play a key role in light-harvesting through the process of photosynthesis, they make up 8 – 14% of the biomass in red, green, and brown seaweeds (Priyadarshani and Biswajit 2012; Mulders et al., 2014). They can be further classified into primary or secondary carotenoids depending on their metabolism and function. Primary carotenoids are the structural and functional components that aid in photosynthesis while the extra-photosynthetic pigments produced by carotenogenesis under specific environmental circumstances are referred to as secondary carotenoids (Kumar et al., 2021). Primary carotenoids include α-carotene, β-carotene, neoxanthin, violaxanthin, zeaxanthin, fucoxanthin, and lutein, whereas secondary carotenoids include echinenone, canthaxanthin, and astaxanthin (Poojary et al., 2016). Carotene is a key precursor of vitamin A, which prevents night blindness and cataracts. It also aids in glycoprotein formation, mucus secretion from epithelial tissues, cell differentiation, overall bone and body development and reproduction, properties that could be valuable in enhancing poultry productivity (Kumar et al.,

TABLE 3 Bioactive compounds present in various seaweeds.

Seaweed type	Bioactive compounds	References
Ecklonia cava	Fucoidan, phlorotannin	Athukorala et al. (2006); Li et al. (2011)
Ulva spp.	Ulvan	Kumar et al. (2021)
Agarum cribosum	Flavanoids, phytosterols	Choudhary et al. (2021)
Fucus vesiculosus	Phlorotannins, fucoidans, fucoxanthin	Holdt and Kraan (2011)
Undaria pinnatifida	Fucoidan, iodine, carotenoids, fucoxanthin, phlorotannins	Li et al. (2011); Poojary et al. (2016)
Ascophyllum nodusum	Fucoidan, alginate, phlorotannins	Shukla et al. (2019)
Dictyota dichotoma	Laminaran	Malyarenko et al. (2019)
Sargassum spp.	Carotenoids, fucoxanthin	Poojary et al. (2016)
Laminaria spp.	Laminaran, alginate, mannitol	Li et al. (2011); Kumar et al. (2021)
Chondrus crispus	Carrageenan	Kumar et al. (2021)
Saccharina japonica	Iodine, carotenoids, fucoxanthin	Poojary et al. (2016); Kumar et al. (2021)

2021). Carotenoids impart important functional utility to seaweed meals through their antioxidant and immune-boosting properties, which may reduce cardiovascular disease, inflammation, neurological disorders, obesity, cancer, and age-related muscle diseases (Borowitzka and Borowitzka, 1987; Dutta et al., 2005; Perusek and Maeda, 2013; Miyashita et al., 2020) in a variety of animals and animal models. According to Henriquez et al. (2016), the Chlorophyceae family, which includes *Chlamydomonas*, *Chlorella*, *Dunaliella*, *Haematococcus* and *Muriellopsis* spp., is the major source of carotenoids. They have the most pigment diversity and are the only group that overproduces secondary carotenoids in response to stressful growing conditions to provide photoprotective functions (Mulders et al., 2014).

Carrageenan

Carrageenan is a naturally occurring anionic sulfated linear polysaccharide found in *Chondrus cripus*, *Euchema*, *Gigartinastellate*, *Iridaea*, *Hypnea*, *Solieria*, *Agardhiella*, and *Sarconema* red seaweeds of the Rhodophyceae family (Prajapati et al., 2014). The polysaccharide chains are made up of sulphate half-esters that are linked to sugar units. McHugh (2003) stated that carrageenan comes in various chemical structures and characteristics, depending on the amount and position of the SO_3–groups. These compounds are classified into kappa, lambda, and iota forms, which all contain about 22 – 35% of the sulphate groups (Prajapati et al., 2014). Carrageenan is a versatile ingredient that has no nutritional value, but it can be used in both food and non-food industries (Van de Velde et al., 2002). It has recently been used in the pharmaceutical industry as an excipient in pills and tablets, as well as a potent raw material for hydrogels, due to its putative anti-tumour, immunomodulatory, antiviral, anti-inflammatory, anticoagulant, and antithrombotic properties (Wang et al., 2019) that could support immune responses and protect

poultry from debilitating pathogenic infections and could also play a role as an alternative for in-feed antibiotics.

Fucoidan

Fucoidan is a sulfated polysaccharide found in the cell walls of brown seaweeds (Phaeophyceae). The chain is made up of fucose as the primary monosaccharide, together with varying amounts of galactose, mannose, xylose, rhamnose, and glucuronic acid residues (Ponce and Stortz, 2020). It is a polymer made up of 1,2-linked L-fucose-4-sulfate units and, in rare circumstances, 1,3- or 1,4-linked fucan sulphate with side chains of galactose, uronic acid, and xylose residues (Kumar et al., 2021). Lim and Wan Aida (2017) stated that the chemical structures and composition of this sulfated polysaccharide vary substantially based on geographical location, species, seasons, and population age of seaweed. Commercially, fucoidans are extracted from *Ascophyllum nodosum*, *Ecklonia cava*, *Fucus vesiculosus*, *Saccharina longicruris*, and *Undaria pinnatifida* brown seaweeds (Athukorala et al., 2006). Fucoidan also exhibits strong and important biological bioactivities, which include antiviral, antitumoral, antioxidant, anticoagulant, immunomodulation, antithrombotic, anti-complement, and anti-proliferative properties (Wang et al., 2019; Saeed et al., 2021) with potential utility as immune-boosters and growth promoters in birds.

Phlorotannins

Phlorotannins are a class of polyphenolics biosynthesized *via* the acetate malonate pathway as secondary metabolites in brown seaweeds. They are found either in free form or in complexes with various cell wall components such as alginic acid (Li et al., 2017). Phlorotannins are primarily derived from phloroglucinol (1,3,5-trihydroxy benzene) units with varying degrees of

polymerization and a group of heterogeneous polymeric compounds. In general, phlorotannins are divided into four subclasses based on the mode of linkage: ether (fuhalols and phlorethols), phenyl (fucols), ether and phenyl (fucophlorethols), and dibenzodioxin linkages (eckols) (Yotsu-Yamashita et al., 2013). Various phlorotannin compounds, such as bieckol/dieckol, phlorofucofuroeckol, fucophloroethol, fucodiphloroethol, fucotriphloroethol, and 7-phloroeckol, have been found in brown seaweeds such as *Ascophyllum nodosum*, *Gongolaria usneoides*, *Fucus spiralis*, *Gongolaria nudicaulis*, *Pelvetia canaliculata*, *Ericaria selaginoides*, *Fucus vesiculosus*, and *Saccharina longicruris* (Ferreres et al., 2012). Seaweed phlorotannins have eight interconnected rings in their structure, making them powerful free radical scavengers (Rajauria et al., 2017). As a result, phlorotannins have antibacterial, anti-inflammatory, antioxidant, antivirus, antidiabetic and antiallergic properties (Tong et al., 2021) that could be useful for poultry health and growth performance.

Ulvan

Ulvan is a cell wall polysaccharide that constitutes about 9 to 36% DM of green seaweeds (*Ulva* spp.) (Kidgell et al., 2019). It is primarily made up of sulphate (12.8 – 23%), rhamnose (12.7 – 45%), xylose (2 – 12%), and uronic acids (6.5 – 26.0%) (Yaich et al., 2017). *Ulva* species have three other cell wall polysaccharides (cellulose, glucuronan and xyloglucan), which together account for up to 45% of their dry weight (Lahaye and Kaeffer, 1997). The ulvan backbone is often composed of α- and β-(1,4)-linked monosaccharides (rhamnose, xylose, uronic acid) with repeating disaccharide units. Aldobiuronic acids (types A and B) are the two primary disaccharide repeating units, while ulvanobioses (type U) are the minor disaccharide aldobioses. Type U ulvanobioses are significantly less prevalent than types A and B (Kidgell et al., 2019). In this regard, ulvan could be used to produce biomaterials (for tissue engineering, wound dressings, excipients, and biofilm prevention), nutraceuticals, and functional foods (Alves et al., 2013; Venkatesan et al., 2015; Cunha and Grenha, 2016).

Laminarins

Laminarins are a type of low-molecular-weight storage β-glucan that is made up of 1,3-β-$_D$-glucan linkage (Rioux et al., 2007). They are made up of (1,3)-β-D-glucopyranose residues with some 6-O-branching in the main chain, as well as some β-(1,6)-intrachain linkages (Kadam et al., 2015). *Laminaria hyperborea* and *Laminaria digitata* produce two types of laminarans, the soluble and insoluble forms, depending on solubility in cold water. Two chains, M and G, are generated based on the amount of mannitol present in both laminarans,

with mannitol residues occupying the reducing terminal area in M-chains and glucose residues occupying the terminal region in G-chains (Kumar et al., 2021). Environmental factors such as nutritive salts and frond age influence the structure and ratio of the two forms of laminarin (Chizhov et al., 1998). In addition, the composition of laminarin is also affected by other environmental parameters such as water temperature, salinity, waves, sea current, and depth of immersion (Kadam et al., 2015). These factors are also thought to affect laminarin's biofunctional activities (Rioux et al., 2010), which include antitumor, anticoagulant, anti-inflammatory, anti-apoptotic, and antioxidant activity (Kadam et al., 2015).

Current evidence of seaweed utilization in poultry diets

Feed utilization and growth performance

Over the last two decades, the poultry industry has experimented with seaweeds as novel dietary additives supplying prebiotics, pigments, polyunsaturated fatty acids, and other bioactive compounds that could be beneficial to growth performance and health of birds (Evans and Critchley, 2014). Table 4 provides a summary of some *in vivo* outcomes when seaweeds have been included in poultry diets. Michalak and Chojnacka (2015) reported that seaweed bioactive components can improve chicken performance and health while also increasing the quantity and quality of eggs and meat produced. Indeed, Kulshreshtha et al. (2020) stated that one of the main goals of dietary supplements for poultry is to improve feed efficacy for cost-effectiveness and improved poultry health. A study by Kumar (2018) reported that broilers fed a diet supplemented with 40 g/kg *Sargassum wightii* powder had higher final liveweight (2408 g/bird) compared to birds on the control diet (1364 g/bird). The positive effects of *S. wightii* powder on feed utilization efficiency and weight gain are attributed to its palatability and high nutrient content as well as its ability to improve digestion and absorption of nutrients in the gut. The positive effects on the broilers could be partly due to the presence of essential amino acids, minerals, sterols, vitamins, fucoidan and long chain fatty acids in *S. wightii* powder (Kumar, 2018). Similarly, the use of macroalgae *S. muticum* as a functional feed ingredient (0, 50, 100 and 150 g/kg) in broiler chickens resulted in marginal linear increases in ADG (1.54, 1.93, 1.96, and 1.97 g/bird, respectively) and improvements in feed utilization as measured by FCR (2.17, 0.54, 0.69 and 0.72, respectively) (Erum et al., 2017). In contrast, the inclusion of graded levels (up to 35 g/kg) of green seaweed (*Ulva* sp.) in Cobb 500 broiler chickens was reported to reduce the overall feed conversion efficiency with an FCR of 0.490 in control birds compared to 0.533 in birds consuming diets containing 35 g/kg seaweed (Matshogo et al., 2020). This was

attributed to the presence of non-starch polysaccharides like cellulose and hemicellulose in seaweeds, which would have interfered with the digestion and nutrient absorption processes in chickens. Considering that most seaweeds contain significant quantities of these non-starch polysaccharides, strategies such as the use of extracts or pre-digestion with exogenous fibrolytic enzymes should be explored to optimize the use of seaweed bioactive compounds for sustainable poultry production.

Carcass characteristics and meat quality

In commercial poultry production systems, birds are bred for quick growth, larger breast weight, and enhanced muscle mass and meat quality, which are important factors for consumers when making meat purchasing decisions (Michalak and Mahrose, 2020). In general, seaweeds have a positive impact on meat quality, which includes a reduction in total fat content (Michalak and Mahrose, 2020). However, Bonos et al. (2017) discovered that adding *A. nodosum* (5, 10, and 20 g/kg) to the diets of broiler chickens did not affect the content of monounsaturated, polyunsaturated, and total saturated fatty acids in the breast and thigh meat. El-Naga and Megahed (2018) reported that adding brown seaweed (*A. nodosum*) extract in drinking water (1 mL/L) enhanced breast width and length, dressing color, and reduced body fat in Indian River chicks compared to the control. Similarly, Erum et al. (2017) discovered that incremental dietary levels of *S. muticum* powder reduced the fat pads in broiler birds when 150 g/kg of the powder was added into the diets, a desirable outcome in terms of carcass quality. Simultaneously, meat color changed from yellowish to reddish as the dose of *S. muticum* increased up to 150 g/kg, which was an undesirable outcome given that consumers prefer pale to pink raw meat (Fletcher, 2002; Wideman et al., 2016). However, changes in poultry meat color could be influenced by various other factors such as pre-slaughter and slaughtering procedures (Fletcher, 2002). Kumar (2018) recorded improved carcass traits (leg, thigh, breast, and dressing weights) as the level of brown seaweed (*S. wightii*)

increased (0, 10, 20, 30, and 40 g/kg) in broiler diets. *Sargassum* doses of 10 and 20 g/kg had the greatest supplemental benefit, which was linked to the minerals, vitamins, polyunsaturated fatty acids, essential amino acids, sterols, and polysaccharides found in the seaweed. Contrary to these findings, Cañedo-Castro et al. (2019) reported no significant variations in carcass weights and yield of Arbor Acres broilers given increasing dietary levels of air-dried and ground *Ulva rigida* (0, 20, 40, and 60 g/kg).

Egg production and quality

Egg production and quality are important criteria for laying hen producers and have important economic implications. When seaweeds are used as feed supplements, they can improve both the biochemical and physical indicators of egg quality, which are important for egg producers and consumers (Michalak and Mahrose, 2020). In a recent study by Zewei et al. (2019), Japanese quail-fed diets supplemented with sun-dried and ground green (*Ulva fasciata*) and brown (*S. cinereum*) seaweeds (15 and 30 g/kg, respectively) produced eggs with lower total lipids (364.00 – 386.67 mg/g) and cholesterol (176.33 – 189.33 mg/g) content in the yolk compared to the control eggs (434.67 mg/g total lipids and 211.00 mg/g total cholesterol). In addition, Wang et al. (2013) observed that dietary inclusion of *Enteromorpha prolifera* (10, 20 and 30 g/kg) improved the shell thickness of Highland brown eggs, which was likely due to an increase in calcium content of the shell (Choi et al., 2018). The abundance of sulfates in ulvan isolated from *Ulva* sp. can explain the considerable improvement in eggshell strength of Hy–Line Brown hens (Li et al., 2018). Dietary supplementation (0, 2.5, and 5 g/kg) with the brown seaweed (*A. nodosum*) improved egg weight, shell weight, and yolk color in Lohmann Lite (70 weeks of age) eggs (Stupart, 2019). Hens in the 2.5 g/kg group had considerably larger eggs (63.82 g) and shell weights (6.34 g) compared to the 5 g/kg (62.04 and 6.13 g, respectively) and control groups (63.11 and 6.31 g, respectively), demonstrating that the lower seaweed inclusion level (2.5 g/kg) improved both the productivity and economic efficiency of egg production

TABLE 4 Some biological effects of including seaweeds in poultry diets.

Seaweed type	Findings	References
Ulva spp.	Inclusion levels up to 35 g/kg improved feed intake and weight but not FCE in Boschveld indigenous chickens.	Nhlane et al. (2020)
Laminaria japonica	Dietary supplementation with 10 g/kg improved FCR in broiler chicks.	Bai et al. (2019)
Polysiphonia spp.	Inclusion levels of up to 120 g/kg did not affect BW, ADG, FC and FCR in ducks, irrespective of the diet form (pellet or mash).	El-Deek and Brikaa (2009)
Ulva lactuca	Substituting 10 and 30 g/kg of corn with green seaweed resulted in minimal variations in BWG, cumulative FC and FCR in broilers.	Abudabos et al. (2013)
Palmaria palmate	Dietary inclusion of 1.5 g/kg had beneficial effects on growth performance, cooking loss, drip loss, diarrhea score, and the fecal microbiome.	Balasubramanian et al. (2019)

(Stupart, 2019). However, while dietary inclusion of 5 g/kg of dried and fermented brown seaweeds (*Undaria pinnatifida* and *Hizikia fusiforme*) increased egg production in Hy-Line Brown hens, this had no effect on indicators of egg and eggshell quality.

Effects of seaweeds on poultry health

There is evidence that seaweeds contain compounds with antimicrobial and antiviral capabilities, as well as immunomodulatory effects, which could boost the health and productivity of poultry (Michalak and Mahrose, 2020). Indeed, when broiler chicken diets were supplemented at 1, 2, 3, and 4 g/kg levels with a brown seaweed derivate, polymannuronate, the cecal microbiome was altered resulting in increased lactic and acetic acid concentration in the cecum and improved ADG, FCR, antioxidant capacity, and immune status of the birds (Choi et al., 2014). Sobotik et al. (2018) reported that the dietary addition of *A. nodosum* (0.5 g/kg of feed) ameliorated the effect of prolonged heat stress without compromising growth performance in broiler chickens. This suggests that *A. nodosum* can be used to improve bird welfare and maintain productivity in heat-stressed birds. Frasiska et al. (2016) studied serum lipid profiles of ducks (22 weeks old) fed a meal comprising of a multi-enzyme pre-treated *Gracilaria* sp. waste at 100, 125, and 150 g/kg. They reported that ducks consuming 125 g/kg pre-treated *Gracilaria* sp. had lower serum triglycerides (80.20 *vs.* 92.54 mg/dL in control ducks), low-density lipoprotein (62.2 *vs.* 103.32 mg/dl in control ducks), and cholesterol (108.24 *vs.* 177.02 in control ducks) and higher high-density lipoprotein (52.57 mg/dL compared to 33.92 mmol/L of the control ducks) levels. This outcome was attributed to the biological effect of *Gracilaria* sp. fiber, which acts as an anticoagulant, antihyperlipidemic, and anti-cholesterol agent (Zhang et al., 2004). Moreover, Cañedo-Castro et al. (2019) reported that the inclusion of *U. rigida* (up to 60 g/kg) as a prebiotic feed additive in broiler diets lowered the serum total cholesterol (126.7 mg/dL) and triglyceride (78 mg/dL) levels compared to the control (140.1 and 93.3 mg/dL, respectively). With regards to intestinal histological changes induced by dietary seaweeds; villi width, height, and length were enhanced in birds fed 20, 40, and 60 g/kg of *U. rigida*-containing diets compared to those on the control diet. This shows that both the feed consumption and growth were positively correlated with an increase in villi size. The increase in the width and height of the villi in chicken intestines is associated with an increase in the digestion and absorption function because of the resultant larger absorption area (Awad et al., 2008). However, some of the discordance observed in results reported from feeding trials with seaweeds could be attributed to variations in factors such as the amount of seaweed supplemented (0.5 g/kg being the minimum and 150 g/kg being the maximum amount reported), particle size (ranging between 0.4 and 2 mm), purity of seaweed, drying

methods (air, sun or oven drying) and subsequent processing, and seaweed species (Kulshreshtha et al., 2020).

Challenges facing seaweed usage in poultry production systems

Supply chain, diseases and pests, and unsustainable usage

Although seaweeds are a ubiquitous natural biomass of the oceans, their accessibility remains a major challenge for poultry producers who are based many miles away from the shorelines. The rising costs of fuel around the world would also render their bulk transportation very expensive and further increase production costs. Wet seaweeds (70 – 90% moisture) that are washed to the shorelines have a very short life span (Maia et al., 2016), and if not collected, they decay and emit hydrogen sulfide to the environment, posing a risk to human and animal health (Smetacek and Zingone, 2013). Reliance on conventionally farmed seaweeds would also be a challenge for resource-poor farmers and would negate the goal of building profitable and sustainable poultry production systems. Moreover, seaweed farming faces challenges of disease outbreaks with most of the commercially important species like *Saccharina*, *Laminaria*, *Kappaphycus*, *Pyropia*, and *Eucheuma* affected by many diseases that are caused by endosymbionts and epibionts, resulting in serious economic losses (Wang et al., 2019). Gachon et al. (2010) observed that the occurrence of diseases is directly linked to intensive large-scale seaweed production, further confirming that reliance on cultivated seaweed would not be sustainable for poultry intensification. Ferdouse et al. (2018) reported that seaweed yields from aquaculture are significantly higher compared to wild harvesting. However, the harvesting of cultivated seaweeds requires proper storage and technology. On the other hand, wild seaweed harvesting can result in several ecological and social consequences if not properly managed (Ferdouse et al., 2018). MacMonagail et al. (2017) reported that over 800 000 t of seaweeds are harvested from natural beds every year with minimal consideration of their sustainability. Thus, over-exploitation associated with increased harvesting pressures to meet commercial demand has led to deterioration of seaweed beds (MacMonagail et al. 2017) and may consequently interfere with its supply chain.

Fibre content

Although several studies have reported positive results with regards to the use of various seaweeds in poultry feeds (Øverland et al., 2019), some reports indicate undesirable outcomes such as reduced feed conversion efficiency in broilers (Matshogo et al., 2020) and a lack of improvement on chicken meat shelf-life

indicators (Nhlane et al., 2021). This is because the nutritional composition of seaweeds is highly variable between and within species, with inorganic elements ranging from 11 to 55% on a DM basis (Biancarosa et al., 2017; Øverland et al., 2019). Seaweeds also contain high dietary fibre levels (25 – 75% DM), which are dominated by many non-starch polysaccharides. According to Choudhary et al. (2021) seaweed polysaccharides form an integral part of their cell wall matrix that assist them to survive the harsh environmental sea conditions. However, the rigidity of the cell wall matrix in seaweeds suppresses the release and bioavailability of bioactive substances (Wells et al., 2017) and exhibit a hindering effect that reduces seaweed nutrient digestibility (Tenorio et al., 2018). Ruocco et al. (2016) classified seaweed polysaccharides into structural cell wall, intracellular mucilage, and storage polysaccharides, with the structural polysaccharides reported to be a major challenge for poultry birds. This often requires costly cell wall disruption techniques, thus limiting the usage of seaweed by resource-poor farmers. Indeed, the presence of non-starch polysaccharides (chitosan, fucoidan, cellulose, hemicellulose, and alginate) in the cell wall matrix of seaweed could limit their utility in poultry feeds, especially when included at higher levels in diets. Although the use of seaweed extracts can potentially eliminate the need for pre-treatment methods, Lam (2007) reported that the extraction (except for water extraction) of bioactive compounds from the seaweeds is labor intensive, time consuming, and expensive, and may only be available to resource-rich poultry producers. These extraction processes also require highly skilled personnel to ensure that labile bio-compounds such as carotenoids and polyphenols are not destroyed during the process, especially when thermal treatments are applied (Ummat et al., 2021).

Fishy odor and heavy metals

The fishy odor of seaweeds, which is caused by the presence of 1-octene-3-ol, heptanal, hexanal, nonanal, and hexanol, can affect the aroma, taste and, ultimately, the overall acceptance of poultry products from birds reared on seaweed-containing diets (Peinado et al., 2014). This would necessitate raising awareness about the benefits associated with the consumption of poultry products from birds that were previously reared on seaweed-based diets. Gopi et al. (2020) also reported that seaweeds accumulate high concentrations of minerals and heavy metals (Pb, Cd, AS, and Hg) due to the increasing marine pollution, which in turn could affect the utilization of seaweed by poultry birds. Makkar et al. (2016) reported that these heavy metals could be detrimental to animal and human health. Consequently, there has been research attempts to reduce excess minerals and detoxify heavy metals using microorganisms (e.g., *Lactobacillus*) that transform heavy metals into less toxic forms (Abdel-Megeed, 2021). The accumulation of heavy metals by seaweeds has necessitated

strict cultivation practices in compliance with coastal management policy (Froehlich et al., 2019). The use of heavy metal-rich seaweeds for poultry production, especially at higher dietary inclusion levels, would require pre-processing strategies that reduce the concentration of heavy metals and other antinutrients. Lastly, seaweeds are not a familiar bioresource for many poultry producers in Africa, especially those who live far away from coastal areas.

Enhancing the utility of seaweeds for sustainable poultry production

Potential for seaweed extracts

Apart from the logistical problems affecting the accessibility and utilization of seaweeds as functional ingredients in poultry feeds, their complex cellular structure remains a major problem for efficient utilization in poultry diets. To resolve this challenge, bioactive compounds that are bound in the seaweed cell wall matrix can be extracted and used in poultry diets. Serive et al. (2012) proposed a biorefinery approach to ensure sustainable exploitation of seaweeds. Indeed, green solvents (such as water, ionic liquids, deep eutectic solvents, and subcritical and supercritical fluids) and novel extraction technologies have been developed to sustainably produce safe and high-quality seaweed extracts and eliminate the use of unsafe petroleum derived solvents (Gomez et al., 2020). These novel extraction techniques can be categorized as physical, biological, chemical, or combinations. They include techniques that have been widely used to extract a wide range of bioactive agents such as ultrasound-assisted extraction, microwave-assisted extraction, enzyme-assisted extraction, pressurized liquid extraction and supercritical fluid extraction (Kadam et al., 2015). In addition to their extraction efficiency, these technologies also reduce the extraction time, eliminate the use of toxic chemical solvents, and, as a result, enhance the quality and yield of the extract (Kadam et al., 2015). The seaweeds can be dried, milled, extruded, or mechanical pressed prior to the extraction process that may include heating, pressurized liquid extraction, microwave-assisted extraction, ultrasonication, and supercritical fluid extraction. Moreover, chemical extraction methods that involve the use of organic and inorganic solvents can be employed to further extract seaweed bioactive substances, but it should be noted that the efficiency of the extraction would depend on the polarity, viscosity, surface tension, dielectric constant and dipole moment of the solvent used (Belwal et al., 2018). This will in turn affect the yield and biological activity of the extract, thus it is imperative to choose an extraction technique and an appropriate solvent based on the bioactive substance of interest and their envisioned end application. Seaweed cell wall matrix can also be modified using compression puffing, which is a physical pre-treatment

technique that simultaneously employs heat and pressure, resulting in the alteration of physicochemical properties. Huang et al. (2016) reported that compression puffing of brown seaweed (*S. glaucescens*) improved the extraction of sulphated polysaccharide, fucoidan. The disruption of the cell wall occurs through the process of electroporation, where pores are formed in cell membranes leading to increased permeability (Bryant and Wolfe, 1987). Vorobiev and Lebovka (2015) added that high permeability causes diffusion of the solvent into the cell membranes, which enhances the extraction of the target compound. Bead milling techniques have also been shown to improve protein extraction from seaweed (*Ulva* and *Gracilaria* spp.) compared to other extraction methods alkaline and ultrasound treatment (Kazir et al., 2019). Optimization of the extraction process is critical, not only to reduce cost of extraction, but also to ensure that the target bioactive compounds are efficiently extracted without significant alterations to the biological activities when eventually incorporated into poultry diets.

Enhancing the *in vivo* utilization of seaweed meals

Where poultry producers lack the resources and capacity to extract bioactive compounds, the seaweed meal (dried and milled into a powder) is often incorporated into poultry diets. While this is a less costly and more practical approach, the bioavailability of nutrients and bioactive compounds in seaweed meal to birds can be compromised by its other constituents such as fibre and ash. To improve the utilization of seaweed meals in poultry diets, several strategies such as washing, fermentation, ensiling, and pre-treatments with exogenous enzymes can be employed.

Exogenous enzyme pre-treatments

Wijesinghe and Jeon (2012) noted that cell wall matrix of seaweed is more difficult to hydrolyze, which suggests a need to employ multi-enzyme polysaccharidases to target the various long-chain polysaccharides present in seaweeds. However, Matshogo et al. (2021) observed a lack of improvement on feed utilization, physiological parameters, and meat quality in broiler chickens reared on diets containing seaweed (*Ulva* spp.) that was pre-treated with a combination of protease and fibrolytic enzymes. The lack of dietary differences could have been due to many reasons such as limited hydrolysis time, pH of the enzyme-substrate mixture, or low proportion of enzyme in relation to substrate/fibre levels of the diets. Stokvis et al. (2022) reported a reduction in nutrient digestibility in broilers fed with 2.5 and 5% seaweed (*Ulva laetevirens*) treated with proteolytic enzyme. Contrary to these findings, Trivedi et al. (2015) observed that the treatment of seaweed (*Ulva fasciata*) with cellulase (10 U/g) derived from the

marine fungus, *Cladosporium sphaerospermum* for 24 h at 40°C and pH 4 successfully hydrolyzed crystalline cellulose microfibrils to produce the maximum yield of sugar (112 ± 10 mg/g dry weight). Nonetheless, there are still unacceptable levels of contradictions with regards to the effects of exogenous enzyme pre-treatments of seaweed on poultry performance, especially considering that this strategy is rather costly.

Microbial fermentation

Fermentation, in a solid or liquid state, is another method that can be used to enhance the aroma, texture, taste, flavour, and the shelf life of seaweeds through microbial enzymatic activities and the resultant secondary metabolites (Admassie, 2018; Reboleira et al., 2021). The fermentation of seaweed (*Saccharina japonica*) with *Aspergillus oryzae* and *Monascus* spp. has been reported to reduce the concentration of iodine and heavy metal content (Bruhn et al., 2019) and increase its antioxidant and anti-inflammatory activities (Lin et al., 2016). This suggests that the use of fermented seaweed in poultry diets could improve growth parameters and the keeping quality or shelf life of the meat. Solid-state fermentation of seaweeds has been reported to increase nutrient utilization (Rafiquzzaman et al., 2015), which could be through the unique mycelial growth pattern of molds that allows them to penetrate the cell wall matrix and release nutrients and bioactive compounds. Other studies have indicated that fermentation can hydrolyze higher molecular weight proteins into lower molecular weight oligopeptides and break down peptide bonds to release amino acids, thereby increasing the digestibility of the protein (Ketnawa and Ogawa, 2019; Mohapatra et al., 2019). Fermentation of seaweeds can also be conducted to reduce the compounds that are responsible for off-flavors and thus enhance compounds that are beneficial for aroma and taste through a series of oxidation, degradation, condensation, and polymerization reactions (Feng et al., 2021). This could consequently improve palatability of the diets leading to higher voluntary feed intake. Fermentation, through microbial hydrolysis reactions, could also liberate phenolic compounds (phlorotannins) that are usually bound to carbohydrates (Hur et al., 2014) and thus increase their antioxidant and antimicrobial activities (Campbell et al., 2020) leading to improved poultry product quality. The presence of phenolic compounds like phlorotannins can also suppress microbial degradation and ultimately hinder fermentation processes creating unfavorable fermentation outcomes. However, it is also important to note that phlorotannins can also be beneficial compounds due to their antioxidant properties, thus any tannin-amelioration strategy to improve substrate fermentation e.g., the use of tannin-binding agents, requires careful consideration.

Ensiling

As already mentioned, fresh seaweeds deteriorate rapidly if not dried. Thus, pre-treatment strategies like ensiling have been

commonly used to preserve many forages, especially for ruminants. This could be the reason why there is currently limited knowledge on the characteristics and feed value of seaweed silages (Campbell et al., 2020) in poultry birds. The ensiling of seaweed is a potential strategy to enhance its preservation and consequently promote all-year-round supply of the biomass (Bach et al., 2014). It can also eliminate the need to employ different drying methods and the labor costs associated with drying. Further, it can reduce the challenges that come with sun drying, especially in areas where climatic conditions are unfavorable (Yen et al., 2022). Indeed, Campbell et al. (2020) stated that ensiling is an effective method to preserve seaweeds for animal feed applications. This occurs through anaerobic fermentation where lactate-producing bacteria convert sugars into lactic acid, whose accumulation reduces the pH of ensiled material thereby preserving it (Yen et al., 2022). This has been reported to prevent nutrient losses and microbial (*Enterobacteria* and *Clostridia*) spoilage of seaweed (Herrman et al., 2015). However, Herrman et al. (2015) reported fermentation challenges due to high-buffering capacity, high levels of long-chain polysaccharides (resistant to microbial degradation), and poor natural lactic acid-producing microflora in fresh seaweeds. Despite the obvious benefits that ensiling could bestow on the keeping quality and nutritional value of seaweeds, studies where seaweed silage has been evaluated in poultry nutrition are very limited. A recent study by Stokvis et al. (2021) found that ensiling *Saccharina latissima, U. lactuca*, and *L. digitata* increased crude protein content, but reduced the ash content and *in vitro* organic matter digestibility of the fermented substrate. When ensiled seaweeds were included in broiler diets, no improvement in feed utilization efficiency and final body weight was observed, possibly due to poor organic matter digestibility. The ensiling of seaweeds for poultry nutrition requires further experimentation to optimize the process and nutritional value of the product. In addition, there is very limited data on the impact of including ensiled seaweeds in poultry diets on meat quality and bird health. Indeed, Campbell et al. (2020) proposed that additional research should be carried out on microbiome dynamics during ensiling as well as on the effects of inoculants on quality of seaweed silage.

Washing

The utility of seaweeds can also be improved using cost-effective treatments such as washing with freshwater and various aqueous solutions to reduce high levels of inorganic elements (15% DM salt and heavy metals) and other impurities that are intrinsically bound to seaweeds (Milledge and Harvey, 2016). However, there are very few studies that have evaluated the efficacy of these methods in improving the feed value of seaweed for poultry (Kawai and Murata 2016). High levels of ash in seaweeds can also be reduced using aqueous alkali carbonate solution (Tippmer et al., 1978) or by washing using tap water (Milledge et al., 2018). The effectiveness of these simple strategies needs to be evaluated in feeding trials with poultry birds.

Conclusions and prospects

This review has described the incredible array of nutritive and bioactive compounds that are present in seaweeds and explored how they can be exploited as part of sustainable poultry production systems of the future. There is amble evidence that including seaweeds in poultry diets enhances feed utilization efficiency, growth performance, and meat stability and quality. However, contradicting results on the effect of dietary seaweeds on growth performance and carcass and meat quality traits were unearthed and these require careful consideration and further investigations. In particular, the optimum level of seaweed meal inclusion in diets tends to vary with seaweed and poultry species but in most cases does not exceed 15% (w/w) due to antinutritional effects of fibre and some phenolics. While there are several challenges that face seaweed exploitation as a dietary component in sustainable poultry production systems, this paper reviewed several possible strategies such as enzyme supplementation, tannin amelioration, ensiling, solid-state fermentation, and use of extracts that can be used to overcome them. These strategies should allow for increased use of seaweed bioactive compounds to create functional poultry diets and thus create a "symphony of good things" in the form of economically, socially, and environmentally sustainable poultry production systems of the future. The use of seaweed extracts, instead of seaweed meal, appears more promising in terms of potency and uniform outcomes despite the associated high cost. Further research, especially to optimize extraction of bioactive compounds, is needed to make seaweed a significant dietary component in commercial poultry production. This approach will also ensure uniform outcomes in terms of bird health, growth performance, and meat quality.

Author contributions

VM and CM conceptualized the review. TM, GM, CM, and VM were equally involved in the write-up, editing, and formatting of the review paper. All authors contributed to the article and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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