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REVIEW

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Current knowledge and future perspectives of the use of seaweeds for livestock production and meat quality: a systematic review

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Abstract

The effects of dietary macroalgae, or seaweeds, on growth performance and meat quality of livestock animal species are here reviewed. Macroalgae are classified into *Phaeophyceae* (brown algae), *Rhodophyceae* (red algae) and *Chlorophyceae* (green algae). The most common macroalga genera used as livestock feedstuffs are: *Ascophyllum*, *Laminaria* and *Undaria* for brown algae; *Ulva*, *Codium* and *Cladophora* for green algae; and *Pyropia*, *Chondrus* and *Palmaria* for red algae. Macroalgae are rich in many nutrients, including bioactive compounds, such as soluble polysaccharides, with some species being good sources of n-3 and n-6 polyunsaturated fatty acids. To date, the incorporation of macroalgae in livestock animal diets was shown to improve growth and meat quality, depending on the alga species, dietary level and animal growth stage. Generally, *Ascophyllum nodosum* can increase average daily gain (ADG) in ruminant and pig mostly due to its prebiotic activity in animal's gut. *A. nodosum* also enhances marbling score, colour uniformity and redness, and can decrease saturated fatty acids in ruminant meats. *Laminaria* sp., mainly *Laminaria digitata*, increases ADG and feed efficiency, and improves the antioxidant potential of pork. *Ulva* sp., and its mixture with *Codium* sp., was shown to improve poultry growth at up to 10% feed. Therefore, seaweeds are promising sustainable alternatives to corn and soybean as feed ingredients, thus attenuating the current competition among food-feed-biofuel industries. In addition, macroalgae can hinder eutrophication and participate in bioremediation. However, some challenges need to be overcome, such as the development of large-scale and cost-effective algae production methods and the improvement of algae digestibility by monogastric animals. The dietary inclusion of Carbohydrate-Active enZymes (CAZymes) could allow for the degradation of recalcitrant macroalga cell walls, with an increase of nutrients bioavailability. Overall, the use of macroalgae as feedstuffs is a promising strategy for the development of a more sustainable livestock production.

KEYWORDS
growth performance, macroalgae, monogastrics, ruminants, sustainability

Mónica Costa, Carlos Cardoso should be considered to have equal contribution.

1 | INTRODUCTION

The growing of global population and increased income is estimated to double the overall demand for animal-derived products by 2050 (FAO, 2007), and the most worldwide consumed meats, pork and poultry meat are expected to suffer major impacts. These aspects will negatively influence livestock agriculture due to the overexploitation of corn and soybean food crops, which are the two main conventional feedstuffs for animal feeding (FAO, 2011). Thus, a worsen scenario for land degradation, water deprivation and climate changes is expected, together with an enhanced competition between livestock feed and human food and a scarcity of biofuel natural resources. Therefore, more sustainable dietary ingredients for livestock and biomass for biofuel production are necessary. Macroalgae, commonly named seaweeds or marine algae, represent alternatives to conventional feedstuffs (Makkar et al., 2016) and are a valuable biofuel resource (Herrmann et al., 2015; Langlois et al., 2012).

Macroalgae are multicellular algae with high-growth rates, classified into three main groups according to their chemical composition: *Phaeophyceae* (brown algae), *Rhodophyceae* (red algae) and *Chlorophyceae* (green algae). The most common genera include: *Ascophyllum*, *Laminaria*, *Macrocystis*, *Nereocystis*, *Saccharina*, *Sargassum* and *Undaria* for brown algae; *Chaetomorpha*, *Cladophora*, *Codium* and *Ulva* for green algae; and *Chondrus*, *Gracilaria*, *Palmaria*, *Porphyra* and *Pyropia* for red algae (Lozano, Wacyk, Carrasco, & Cortez-San Martín, 2016; Makkar et al., 2016). The various applications of macroalgae, including animal feed, human food, pharmaceutical industries, organic fertilizers, eutrophication inhibition, bioremediation and biogas generation (Makkar et al., 2016), can explain the predominance of algal cultivation overproduction of algae collected from the wild in the last decade (FAO, 2016).

The use of macroalgae as feedstuff allows the provision of numerous vitamins, bioavailable minerals, pigments (*e.g.* carotenoids and chlorophylls), phenolic compounds (*e.g.* phlorotannins), carbohydrates, high-quality proteins (Gupta & Abu-Ghannam, 2011a; Makkar et al., 2016) and n-3 and n-6 polyunsaturated fatty acids (PUFA), such as 16:4n-3, 18:2n-6, 18:3n-3, 18:4n-3 (Cardoso et al., 2017; Kendel et al., 2015) and, for some algal species, 20:5n-3 (eicosapentaenoic acid, EPA) and 22:6n-3 (docosahexaenoic acid, DHA) (Kendel et al., 2015), to livestock. The deposition of n-3 PUFA in meat can exert health benefits for consumers, such as a decreased risk of cardiovascular diseases, conversely to saturated fatty acids (Givens, 2009). In addition, the presence of various bioactive compounds on macroalgae with immune- or growth-stimulating properties, as well as antimicrobial (i.e. polysaccharides) and antioxidant (i.e. α-tocopherol, pigments, polyphenols and vitamin C) activities (Gupta & Abu-Ghannam, 2011a; Plaza, Cifuentes, & Ibáñez, 2008), can enhance animal growth and meat safety with reduction of antibiotic utilization (Evans & Critchley, 2014).

Despite the wide range of seaweed applications, there are some challenges related to alga production and digestibility by animals. Regarding production, some environmental impacts must also be assessed. The use of Integrated Multi-Trophic Aquaculture (IMTA) represents a sustainable system for macroalgae production but improved cultivars and cost-efficient farm systems are necessary for a large-scale production (Kim, Yarish, Hwang, Park, & Kim, 2017). In addition, the application of biorefinery-based production would reduce the cost of fuel with maximum utilization of biomass (Balina, Romagnoli, & Blumberga, 2017). On the other hand, the presence of recalcitrant polysaccharides in macroalgae cell walls with antinutritional effects for monogastric animals, such as poultry and pigs, and a concomitant decrease in efficiency of feed digestion and absorption by trapping valuable nutrients (Øverland, Mydland, & Skrede, 2019), suggests the use of specific Carbohydrate-Active enZymes (CAZymes), which are today well accepted as feed additives to enhance animal digestibility and growth performance. Moreover, although many macroalgae species, particular red seaweeds, have a superior combination of protein quality and content than corn and wheat, the protein content of soybean meal is higher (approximately 24% DM) than that of algae (Mæhre, Malde, Eilertsen, & Elvevoll, 2014), and thus replacement of this ingredient may not be feasible. Additionally, dry processing of algae might destroy essential vitamins for maintaining animal requirements.

The present work reviews the effect of dietary macroalgae on livestock animals' growth performance and meat quality, as well as the potential and constraints of macroalgae inclusion in livestock diets.

2 | MACROALGAE CHARACTERIZATION

Macroalgae comprise a huge number of very diverse live organisms, possibly surpassing 25,000 species (Santos et al., 2015), of macroscopic, multicellular and marine algae (Hurd, Harrison, Bischof, & Lobban, 2014). They belong to three different and relatively unrelated eukaryotic lineages corresponding to taxonomically distant groups, usually termed brown (*Phaeophyceae*), red (*Rhodophyceae*) and green (*Chlorophyceae*) macroalgae. Brown algae contain a distinct chlorophyll composition (types *a* and *c*) and carotenoids (mainly fucoxanthin, which renders these macroalgae brown). Red algae, besides chlorophylls and carotenoids, are rich in phycobilins. Green algae have chlorophylls *a* and *b*, as well as carotenoids, in the chloroplasts (Pereira, 2016). There is a great biological diversity among seaweeds, concerning life cycle and fertilization or morphogenetic strategies. Size is also very different, being some macroalgae up to several meters long and displaying a high level of complexity (Pereira, 2016). However, less than twenty seaweed species comprise 90% of the commercially used biomass per year and worldwide (Pereira, 2016).

Though still small in economic relevance when compared with terrestrial plants ($<30 \times 10^6$ versus 16×10^{11} fresh weight tonnes of biomass, respectively), the commercial interest in seaweeds has grown in the last years (Buschmann et al., 2017). Their production more than duplicated in the last decade, increasing from 14.7 million tons in 2005 to 30.4 million tonnes in 2015, from which 209 394

tonnes were for non-human consumption (FAO, 2018). Promising attempts have been made towards a large scale-algae production, such as naturally floating beds supplied nutrient-rich water, offshore (rafts) or land (coastal deserts) productions. These methods take profit of the fast growth of seaweeds and the absence of requirement of arable land, freshwater or fertilizer for their production (Halmemies-Beauchet-Filleau et al., 2018; Lorbeer, Tham, & Zhang, 2013). The industrial use of macroalgal biomass has evolved in recent years, from exploiting beach-cast macroalgae as fertilizers and a source of potash to hydrocolloid extraction (Buschmann et al., 2017; Synytsya, Čopíková, Kim, & Il Park, 2015). A possible future scenario may involve macroalgae grown for high added-value applications, such as the extraction of particular polysaccharides (Bixler & Porse, 2011) or biomass utilization for specialty agronomic/husbandry products (Craigie, 2011). Further up in the value scale, other applications, such as ingredients for food and feed (Fleurence, 2016), cosmeceuticals (Balboa, Conde, Soto, Pérez-Armada, & Domínguez, 2015), nutraceuticals (Himaya & Kim, 2015) and pharmaceuticals (Anis, Ahmed, & Hasan, 2017; Vo, Ngo, & Kim, 2012), may indeed become very important. In addition, seaweeds can be a valuable tool to respond to the growing concerns about the environment through nutrient cycling with mitigation of water nutrient loading and, thus, preventing eutrophication processes. Moreover, macroalgae contribute to carbon fixation with a consequent reduction of greenhouse gas emissions, including methane released by ruminants (Buschmann et al., 2017).

3 | MACROALGAE PRODUCTION

Macroalgae may be wild-harvested from the Coast or may be cultivated. In Europe, most production comes from wild harvesting. However, due to possible environmental impacts, wild harvesting has declined over the past decade and there is a drive to meet the growing demand by shifting production toward cultivation (van Oirschot et al., 2017).

In any case, macroalgal growth entails consumption of energy and nutrients. Moreover, cultivation may also generate deleterious effects on the environment and these may be intensified by the expansion of the scale of operations (van Oirschot et al., 2017). There are also indirect environmental effects that relate to upstream production of the means required to macroalgal cultivation, and downstream transport, drying, and further processing of the harvested material. The by-products of the processing operations may be directed to production of fertilizer, thus contributing to the mitigation of the environmental impacts. In addition, from an economic point of view, although harvesting is associated to several costs, mainly related to the required labour to collect a widely distributed amount of biomass and the associated licensing expenses, cultivation also entails significant costs. The latter include investments, payment of energy costs (for instance, in order to ensure adequate agitation) and deployment of abundant water resources, which are expensive in many countries. However, some case-studies limited to particular countries have concluded that macroalgal cultivation may be profitable (Hasselström et al., 2020).

There are different systems of cultivation, ranging from purely extensive to very intensive, that should be noted. The latter presupposes a more intense nutrient uptake and a concomitant production of wastewater streams with a high organic load and liable to generate downstream eutrophication issues. Using current technology, extensively available sea areas may be farmed to produce macroalgae that require no freshwater or fertilizers while providing a variety of valuable ecosystem services. Macroalgal cultivation in this environmentally more sustainable form is an extractive industry whose very process of biomass production renders ecological services to the marine ecosystems, thereby also adding economic value (Neori et al., 2009; Radulovich et al., 2015). In particular, the farming of macroalgae in combination with the production of fish and organic extractive feeders (e.g. abalone, bivalves, and sea urchin) is being used to remove the excess of inorganic nutrients from the production system. This concept (IMTA) is gaining importance as a sustainable food production system (Shpigel et al., 2018; Cunha et al., 2019). Kelps (e.g. *Laminaria digitata*), *Ulva* spp., and other macroalgae are being farmed in such integrated modules (Broch et al. 2013; Macchiavello et al., 2014).

The cultivation of macroalgae may also be done in a variety of systems from raceways to settling ponds. Water flow and aeration may be necessary to promote the renewal of the boundary layer between algae and water surfaces, in order to favour the diffusion of the nutrient into the algal biomass (Diamahesa, Masumoto, Jusadi, & Setiawati, 2017). Relying on nutrient concentration and water flow, which can range from one to sixteen water exchanges (per day), it is possible to enhance nutrient uptake and growth (Neori et al., 2003). If the water flow is low, nutrients will become limiting, biomass production will decrease, but the nutrient uptake efficiency will increase (Diamahesa et al., 2017). This may be an alternative, whenever sample space for extensive systems is available.

In addition, the direct and indirect environmental impacts of macroalgal cultivation have been studied and quantified with life cycle assessment (LCA) (Seghetta, Hou, Bastianoni, Bjerre, & Thomsen, 2016). This assessment depends much on the specific materials and design differences between conventional or intensified cultivation designs. Van Oirschot et al. (2017) concluded that there are substantial environmental impacts and that, under specific circumstances, intense systems may offer significant productivity advantages for macroalgal cultivation limited by permits/licenses to small areas. In such cases, an intensification of cultivation systems could augment productivity in such small-designated space, without significantly affecting life cycle environmental impacts (van Oirschot et al., 2017). For the latter, the drying process has the highest contribution. Any macroalgal system requiring the drying of biomass should approach dewatering strategically, entailing a search for innovative uses of the available energy of the oceans (e.g. wind, waves or currents). The adoption of low energy alternatives would be advisable, such as solar dryers. Furthermore, processing of macroalgal biomass into animal feed ingredients may also involve extracting, refining and other separation operations, thereby generating by-product materials (Barbot,

TABLE 1 Protein content and amino acid profile of the main seaweed species used as animal feed (all values are expressed on a dry weight basis, w/dw, unless otherwise indicated; hyphenated values are ranges on the basis of several studies)[†]

Chemical composition	*Ascophyllum* sp. (brown alga)	*Laminaria* sp. (brown alga)	*Undaria pinnatifida* (brown alga)	*Ulva* sp. (green alga)	*Porphyra* sp. (red alga)
Crude protein (%)	5.6–12.1 (8.1)	0.6–16.1 (7.7)	15.7–22.2 (18.2)	4.8–41.8 (15.8)	24.1–44.0 (32.7)
Amino acid profile (% total amino acids)					
Alanine	7.1–8.8 (8.0)	6.8–14.8 (9.6)	5.5–17.3 (10.3)	1.8–10.1 (8.1)	6.8–14.6 (10.5)
Arginine	4.2–12.3 (7.3)	3.9–5.5 (4.8)	4.0–9.9 (6.2)	3.0–11.6 (7.2)	6.6–10.7 (8.0)
Aspartic acid	10.6–12.9 (11.6)	8.4–14.8 (11.5)	6.5–10.9 (9.2)	8.8–15.1 (12.2)	7.9–14.0 (11.1)
Cystine	0.0–2.4 (0.8)	1.4–3.6 (2.9)	0.4–1.5 (0.9)	1.0–7.7 (2.6)	0.5–2.1 (1.6)
Glutamic acid	15.4–22.9 (18.5)	7.0–28.3 (15.5)	6.8–16.9 (13.0)	3.2–23.1 (13.6)	9.8–12.7 (11.8)
Glycine	5.6–7.7 (6.4)	4.8–6.6 (5.9)	4.6–7.4 (5.8)	2.2–8.8 (6.2)	6.6–8.9 (7.3)
Histidine	1.7–2.0 (1.9)	1.5–4.3 (2.4)	1.9–10.0 (4.1)	1.1–4.6 (2.1)	1.3–4.3 (2.5)
Isoleucine	3.9–4.5 (4.2)	3.2–4.7 (4.1)	3.8–5.7 (4.8)	2.8–4.8 (3.9)	3.6–5.4 (4.5)
Leucine	7.1–7.9 (7.4)	5.8–8.4 (7.4)	6.8–9.7 (8.6)	5.0–8.5 (6.9)	6.3–9.7 (8.0)
Lysine	5.7–7.6 (6.3)	4.6–8.6 (6.0)	4.4–7.1 (5.7)	4.1–16.8 (5.8)	3.5–8.6 (6.1)
Methionine	1.1–2.5 (1.9)	1.1–2.9 (2.2)	0.2–3.1 (2.0)	1.5–19.1 (3.5)	1.2–3.0 (2.2)
Phenylalanine	3.5–5.3 (4.5)	3.8–5.5 (4.9)	4.3–6.1 (5.3)	4.4–13.0 (6.1)	4.1–9.3 (5.6)
Proline	4.0–5.3 (4.6)	3.4–6.3 (4.8)	3.5–5.0 (4.3)	3.1–5.7 (4.1)	4.4–5.9 (5.0)
Serine	4.6–5.3 (5.0)	3.9–5.9 (5.1)	3.7–5.5 (4.5)	4.3–6.8 (5.2)	5.3–8.1 (6.2)
Threonine	4.3–5.7 (4.9)	4.2–6.1 (5.5)	3.3–5.4 (4.6)	4.1–6.1 (5.2)	5.8–8.7 (6.8)
Tryptophan	ND[1]	0.3–0.6 (0.5)	0.3–1.5 (0.8)	0.7–0.9 (0.8)	1.1
Tyrosine	1.4–2.2 (1.8)	2.0–3.1 (2.7)	2.4–4.9 (3.3)	1.8–4.8 (2.9)	3.5–5.6 (4.7)
Valine	4.7–5.8 (5.4)	4.5–10.8 (6.5)	4.8–10.7 (6.9)	5.4–7.0 (6.2)	5.7–8.6 (7.1)
Crude carbohydrates (%)	59.1–62.8 (60.9)	35.5–60.7 (48.1)	38.1[2]–52.1 (45.1)	40.3–64.8[3] (49.7)	44.6
Neutral detergent fibre	19.8–22.0 (20.9)	16.3–20.1 (8.2)	15.2–38.1 (26.7)	25.9–41.5 (32.3)	33.5–40.8 (37.1)
Crude fibre	4.1–6.8 (5.5)	7.7	3.2–3.4 (3.3)	2.8–13.8 (7.8)	1.1
Total dietary fibre	57.9	36.1–39.6 (37.8)	30.7–51.4 (37.7)	24.8–40.6 (29.5)	22.9–53.5 (39.8)

Values in parenthesis after inferior and superior ranges correspond to mean values.

Number of observations for crude protein: *Ascophyllum* sp. (n = 6), *Laminaria* sp. (n = 30), *Undaria pinnatifida* (n = 6), *Ulva* sp. (n = 48), *Porphyra* sp. (n = 11).

Number of observations for amino acids: *Ascophyllum* sp. (n = 3), *Laminaria* sp. (n = 6), *Undaria pinnatifida* (n = 5), *Ulva* sp. (n = 11), *Porphyra* sp. (n = 6).

Number of observations for all carbohydrates:*Ascophyllum* sp.(n = 5),*Laminaria* sp.(n = 4),*Undaria pinnatifida* (n = 6), *Ulva* sp. (n = 20),*Porphyra* sp. (n = 7).

[1]not detected.

[2]soluble and insoluble dietary fibre + neutral sugars.

[3]monosaccharides + total dietary fibre.

[†]Supporting literature: Abudabos et al.(2013); Anderson, Blanton, Gleghorn, Kim, & Johnson(2006); Applegate & Gray(1995); Arieli, Sklan, & Kissil(1993); Burtin (2003); Cabrita, Maia, Sousa-Pinto, and Fonseca(2017); Cofrades et al. (2010), Cruz-Suárez, Tapia-Salazar, Nieto-López, Guajardo-Barbosa, & Ricque-Marie(2009); Dawczynski, Schubert, & Jahreis (2007); Dierick, Ovyn, & De Smet (2009); Dierick, Ovyn, & De Smet (2010); Diler, Tekinay, Güroy, Güroy, & Soyuturk (2007); Erickson et al. (2012); Gaillard et al. (2018); Hernández, Uriarte, Viana, Westermeier, & Farias (2009); İrkin & Erduğan (2014); Je et al. (2009); Kolb et al. (2004); Mæhre, Malde, Eilertsen, & Elvevoll (2014); Maia, Fonseca, Oliveira, Mendonça, & Cabrita (2016); Marsham, Scott, & Tobin (2007); Misurcova, Kracmar, Klejdus, and Vacek (2010); Moroney, O'Grady, O'Doherty, & Kerry (2012); Neveux, Magnusson, Maschmeyer, de Nys, & Paul (2015); Okab et al. (2013); Peña-Rodríguez, Mawhinney, Ricque-Marie, & Cruz-Suárez (2011); Ripol et al.(2018); Rjiba-Ktita, Chermiti, Bodas, France, & López (2017); Ruperez & Saura-Calixto (2001); Sánchez-Machado, López-Cervantes, López-Hernández, & Paseiro-Losada (2004); Schiener, Black, Stanley, & Green (2015); Taboada, Millán, & Miguez (2013); Tayyab, Novoa-Garrido, Roleda, Lind, & Weisbjerg (2016); Valente et al. (2006); Wahbeh (1997); Yamada, Miyoshi, Tanada, and Imaki (1991).

Al-Ghaili, & Benz, 2016). This problem may be tackled by the simultaneous production of combustible biomethane, through anaerobic microbial digestion of macroalgae residues, and disposal of undesirable biomass in a synergistic waste management system (Barbot et al., 2016). Seaweed waste by-products have several current applications, including the production of fibre, glycerol, biofertilizers and organic acids, as well as the bioremediation of contaminated waters due to algal adsorbing properties (Barbot et al., 2016).

4 | NUTRITIONAL PROPERTIES

Macroalgae are rich in several nutrients but with different nutritional profiles (Tables 1, 2 and 3), although some general traits are common to all seaweeds. Carbohydrates comprise a very large share of their dry matter (DM) (up to 70%) and lipid fraction is usually lower than 5% DM (Campos et al., 2019; Ripol et al., 2018), with maximum-reported values of 6.6% DM (Wahbeh, 1997).

Some species of brown algae belonging to the genera *Laminaria*, *Saccharina*, *Hizikia* and *Arame* have a lipid content as low

TABLE 2 Lipid content and fatty acid profile of the main seaweed species used as animal feed (all values are expressed on a dry weight basis, w/dw, unless otherwise indicated; hyphenated values are ranges on the basis of several studies)†

Chemical composition	*Ascophyllum* sp. (brown alga)	*Laminaria* sp. (brown alga)	*Undaria pinnatifida* (brown alga)	*Ulva* sp. (green alga)	*Porphyra* sp. (red alga)
Crude fat (%)	2.9-5.8 (3.9)	0.5-1.3 (0.9)	1.1-6.5 (3.4)	0.1-6.6 (2.0)	0.7-3.0 (1.6)
Fatty acid profile (% total fatty acids)					
14:0	8.9-9.4 (9.1)	2.9-9.1 (6.1)	2.3-4.0 (3.1)	0.7-10.9 (3.1)	0.0-4.1 (1.9)
16:0	9.9-13.4 (11.7)	18.0-36.0 (25.5)	13.5-27.7 (19.2)	3.2-50.3 (26.6)	19.3-63.2 (34.6)
17:0	0.41	ND[3]	0.0-0.2 (0.1)	0.1-1.4 (0.5)	0.03-0.2 (0.1)
18:0	0.6-0.8 (0.7)	0.3-1.5 (1.0)	0.7-1.8 (1.1)	0.2-1.8 (0.9)	0.7-1.9 (1.2)
20:0	0.2	ND[3]	0.4-4.9 (2.6)	0.3-6.5 (1.7)	0.2-0.5 (0.4)
22:0	0.2	ND[3]	ND[3]	1.9-5.1 (3.0)	0.4
16:1n−7 + n−9	1.4-2.2 (1.8)[1]	0.9-5.6 (2.6)[1]	0.4-3.7 (2.1)[1]	0.8-9.1 (2.1)	1.0-6.2 (2.8)[1]
18:1n−7 + n−9	28.3-42.0 (35.1)[2]	17.8-26.5 (21.6)[2]	6.8-12.5 (9.6)[2]	3.5-40.5 (11.1)	4.3-8.0 (7.1)
18:1-cis−11	ND[3]	ND[3]	ND[3]	4.7-6.4 (5.5)	ND[3]
20:1 n−7n−9n−11	0.07[4]	1.6[4]	0.0	0.2-2.1 (0.7)	1.4-4.7 (2.6)
16:2n−6	ND[3]	ND[3]	ND[3]	1.4-20.3 (10.8)	ND[3]
16:3n−3	ND[3]	ND[3]	ND[3]	2.0-2.6 (2.3)	ND[3]
16:4n−3	ND[3]	ND[3]	ND[3]	4.8-7.1 (6.0)	ND[3]
18:2n−6	7.5-8.6 (8.1)	5.0-9.5 (7.2)	6.2-8.8 (7.4)	2.4-22.0 (10.2)	1.2-7.1 (3.4)
18:3n−6	0.54	ND[3]	1.7	0.1-5.6 (1.6)	0.3-2.6 (1.7)
18:3n−3	2.4-4.5 (3.4)	0.8-7.5 (4.8)	7.9-12.0 (10.6)	0.1-26.4 (11.3)	0.0-5.7 (1.9)
18:4n−3	ND[3]	1.2-10.8 (7.6)	21.1-25.8 (22.7)	0.2-7.3 (3.6)	0.2-14.0 (4.8)
20:2n−6	5.1	0.9	0.0-0.1 (0.1)	3.0	0.5-1.1 (0.8)
20:3n−6	0.7	1.2	0.6-1.0 (0.8)	1.1-1.5 (1.2)	1.0-1.8 (1.3)
20:4n−6 (ARA)	12.1-17.3 (14.7)	7.0-14.2 (10.2)	13.3-17.5 (15.5)	0.5-2.1 (1.3)	6.4-9.8 (7.5)
20:4n−3	ND[3]	0.54	0.7-1.5 (1.1)	0.1-0.7 (0.4)	0.1-0.5 (0.3)
20:5n−3 (EPA)	5.3-7.2 (6.3)	8.6-16.2 (11.8)	6.0-13.2 (9.4)	0.4-2.6 (1.6)	6.0-43.0 (25.2)
22:4n−6	ND[3]	ND[3]	ND[3]	0.1-0.8 (0.5)	ND[4]
22:5n−3	ND[3]	ND[3]	ND[3]	0.2-2.2 (1.4)	0.05
22:6n−3 (DHA)	0.0	ND[3]	ND[3]	0.2-1.6 (0.5)	ND[4]

Values in parenthesis after inferior and superior ranges correspond to mean values.

Number of observations for crude fat: *Ascophyllum* sp. (n =4), *Laminaria* sp. (n = 6), *Undaria pinnatifida* (n = 4), *Ulva* sp. (n = 49), *Porphyra* sp. (n = 6).

Number of observations for fatty acids: *Ascophyllum* sp. (n =2), *Laminaria* sp. (n = 5), *Undaria pinnatifida* (n = 4), *Ulva* sp. (n = 12), *Porphyra* sp. (n = 6).

[1]only includes 16:1n-7.

[2]18:1n-7 is present in trace amount.

[3]not detected.

[4]includes only 20:1n-9.

†Supporting literature: Abudabos et al. (2013); Arieli, Sklan, & Kissil (1993); Biancarosa et al. (2018); Cabrita, Maia, Sousa-Pinto, and Fonseca (2017); Cardoso et al. (2017); Cofrades et al. (2010); Cruz-Suárez, Tapia-Salazar, Nieto-López, Guajardo-Barbosa, & Ricque-Marie (2009); Dawczynski, Schubert, & Jahreis (2007); Dierick, Ovyn, & De Smet (2009); Dierick, Ovyn, & De Smet (2010); Diler, Tekinay, Güroy, Güroy, & Soyuturk (2007); Erickson et al. (2012); Fleurence, Gutbier, Mabeau, and Leray (1994), İrkin & Erduğan (2014); Lorenzo et al. (2017); Mæhre, Malde, Eilertsen, & Elvevoll (2014); Maia, Fonseca, Oliveira, Mendonça, & Cabrita (2016); Marsham, Scott, & Tobin (2007); Neveux, Magnusson, Maschmeyer, de Nys, & Paul (2015); Okab et al. (2013); Peña-Rodríguez, Mawhinney, Ricque-Marie, & Cruz-Suárez (2011); Ripol et al. (2018); Rjiba-Ktita, Chermiti, Bodas, France, & López (2017); Sánchez-Machado, Lopez-Cervantes, Lopez-Hernandez, & Paseiro-Losada (2004); Taboada, Millán, & Miguez (2013); Valente et al. (2006); Ventura, Castanon, & McNab (1994); Ventura & Castañón (1998); Wahbeh (1997).

TABLE 3 Ash, mineral, pigment and vitamin contents of the main seaweed species used as animal feed (all values are expressed on a dry weight basis, w/dw, unless otherwise indicated; hyphenated values are ranges on the basis of several studies)*

Chemical composition	*Ascophyllum* sp. (brown alga)	*Laminaria* sp. (brown alga)	*Undaria pinnatifida* (brown alga)	*Ulva* sp. (green alga)	*Porphyra* sp. (red alga)
Ash (%)	0.8-30.9 (21.4)	23.3-73.0 (35.7)	17.4-39.8 (29.2)	11.3-49.6 (24.0)	9.3-29.6 (18.0)
Ca (g/kg)	9.8-34.1 (15.3)	0.5-22.8 (11.4)	9.3-10.7 (9.7)	0.3-68.8 (13.2)	0.1-7.0 (4.0)
Cu (mg/kg)	1.6-17.0 (5.7)	1.0-20.0 (5.0)	1.9-6.7 (4.3)	3.4-146.8 (25.6)	<5.0; 8.0-13.6 (10.1)
Fe (mg/kg)	100-370 (201)	11.9-702 (164)	15.4-133 (74.6)	139-5800 (1993)	89.0-182 (134)
I (mg/kg)	461-1136 (770)	277-11096 (5846))	191-306 (252)	8.0-130 (60.2)	22.0-110 (54.3)
K (g/kg)	14.0-87.0 (30.4)	10.0-116 (53.4)	3.3-107 (63.6)	12.0-29.0 (20.2)	14.1-35.0 (23.5)
Mg (g/kg)	5.7-11.4 (8.6)	5.5-8.4 (6.6)	4.1-11.8 (8.1)	11.0-27.0 (20.5)	2.8-17.0 (7.3)
Mn (mg/kg)	10.0-56.8 (21.1)	2.9-38.0 (9.5)	3.3-19.4 (10.0)	11.0-637 (114)	6.7-31.4 (22.7)
Na (g/kg)	27.3-52.0 (38.7)	10.0-38.2 (25.1)	51.6-70.6 (62.4)	5.4-32.8 (12.7)	4.4-100 (38.1)
P (g/kg)	0.5-2.3 (1.1)	1.2-3.0 (2.0)	2.9-4.5 (3.7)	≤ 0.5-6.6 (2.3)	2.5-5.0 (3.6)
S (g/kg)	11.0-35.0 (24.6)	10.0[1]-11.0	9.0	15.4-57.5 (38.8)	19.0
Se (mg/kg)	0.06-< 1.0	0.02-0.94 (0.3)	< 0.5	0.05-1.9 (0.5)	0.17
Zn (mg/kg)	28.0-114 (55.6)	1.0-81.0 (33.5)	9.4-60.8 (33.5)	6.0-63.8 (32.2)	22.1-67.0 (41.1)
Carotenoids (mg/kg)	1.5-1673(737)[1,2]	25.7[1]	54.4	169-2550(1085)[5,8]	72.7[1]-1630
β-Carotene	30.0-700 (260)[4,5]	29.9	13.0	105[9]-163	408
α-Carotene	ND[3]	ND[3]	ND[3]	ND[3]	280
trans-luteines	ND[3]	ND[3]	ND[3]	1848	ND[3]
Zeaxanthin	ND[3]	6.0[1]	8.0[1]	10.2-35.2 (21.3)[1]	817
Fucoxanthin	60.0-525 (295)[4,5]	33.2-213 (145)	682-4960 (2445)		ND[3]
Violaxanthin	12.0-40.0 (26.0)	ND[3]	ND[3]		ND[3]
Chlorophyll (mg/kg)	0.8-1369 (579)[1,6]	174-224[7] (199)[6]	405[1]	368-8500 (5217)	508[1]
Chlorophyll a	0.4-1155 (479)[1]	142-701 (422)[1]	396[1]	254-5000 (3115)[5,8]	500-3300 (1900)[4]
Chlorophyll b	ND[3]	14.0[1]	ND[3]	114[6]	7.2[1]
Chlorophyll c	0.4-214 (99.7)[1]	10.3[1]-48.2[1,7] (29.2)[1]	16.0[1]	ND[3]	ND[3]
Chlorophyll d	ND[3]	15.6[1]	6.6[1]	ND[3]	9.8[1]
Phycobilin (mg/kg)	-	-	-	-	1710-24400 (13055)
Vitamins (mg/kg)					
Vitamin B_1	1.0-27.0 (14.0)	1.4-12.5 (5.0)	3-50.4 (26.7)	7.5-40.0 (23.8)	9.6
Vitamin B_2	5.0-10.0 (7.0)	1.4-8.5 (5.0)	13.5-117 (65.3)	3.8-5.3 (4.7)	34.3
Vitamin B_3	0.0-15.0 (8.0)	15.8-612 (314)	< 5.0; 25.6-900 (463) (310.1)[h]	1000	95.1

(Continues)

TABLE 3 (Continued)

Chemical composition	*Ascophyllum* sp. (brown alga)	*Laminaria* sp. (brown alga)	*Undaria pinnatifida* (brown alga)	*Ulva* sp. (green alga)	*Porphyra* sp. (red alga)
Vitamin B_5	-	-	-	1.7[1]	-
Vitamin B_6	0.13	0.9-64.1 (32.5)	1.8-32.4 (17.1)	< 0.1	14.9
Vitamin B_8	0.13	64.1	1.9	ND[3]	ND[3]
Vitamin B_9	456	0.0-0.5	0.5-66.0 (33.2)	1.5-1080[1]	0.4-125 (62.9)
Vitamin B_{12}	0.001[1]	0.005[1]	0.003-0.04[1]	(0.06-0.063)[1] (0.062)[1]	0.008[1]
Vitamin E	3.6-500 (230)	3.0-2000 (511)	14.0[1]-174	2.8-35.0 (15.6)	10.6-14.3 (12.8)
α-tocopherol	80.0	6.2		8.8	10.1-13.1 (11.6)
Vitamin C	81.0-1650 (604)	355-910 (633)	31.0-1847 (939)	42.0-1250 (511)	1611

Values in parenthesis after inferior and superior ranges correspond to mean values.

Number of observations for ash: *Ascophyllum* sp. (n =8), *Laminaria* sp. (n = 13), *Undaria pinnatifida* (n = 4), *Ulva* sp. (n = 49), *Porphyra* sp. (n = 7).

Number of observations for minerals: *Ascophyllum* sp. (n =11), *Laminaria* sp. (n = 26), *Undaria pinnatifida* (n = 5), *Ulva* sp. (n = 18), *Porphyra* sp. (n = 7).

Number of observations for carotenoids: *Ascophyllum* sp. (n =9), *Laminaria* sp. (n = 10), *Undaria pinnatifida* (n = 8), *Ulva* sp. (n = 12), *Porphyra* sp. (n = 4).

Number of observations for vitamins: *Ascophyllum* sp. (n =4), *Laminaria* sp. (n = 6), *Undaria pinnatifida* (n = 4), *Ulva* sp. (n = 5), *Porphyra* sp. (n = 4).

[1]values are expressed on a fresh weight basis.

[2]sum of clorophyll a, clorophyll c and fucoxanthin.

[3]not detected.

[4]approximate values.

[5]include values of algae thalli.

[6]sum of clorophyll a and clorophyll c.

[7]value obtained from algae rhizoid.

[8]carotenoid content reported on fresh weight basis was converted into dry weight basis estimating moisture content of 80%, according to Eismann, Reis, da Silva, & Cavalcanti (2020).

[9]include total carotene pigments.

[10]total xanthophyll content. Fucoxanthin and *trans*-zeaxanthin described as being absent in Cruz-Suárez, Tapia-Salazar, Nieto-López, Guajardo-Barbosa, & Ricque-Marie (2009).

[†]Supporting literature: Abudabos et al.(2013); Afonso et al.(2018); Arieli, Sklan, & Kissil(1993); Biancarosa et al.(2018); Billakanti, Catchpole, Fenton, Mitchell, and MacKenzie(2013); Cabrita et al.(2016); Cabrita, Maia, Sousa-Pinto, and Fonseca(2017); Cofrades et al.(2010); Corino, Modina, Di Giancamillo, Chiapparini, & Rossi(2019); Cruz-Suárez et al.(2009);Czeczuga & Taylor(1987); Dere, Güneş, & Sivaci(1998); Desideri et al.(2016); Diler, Tekinay, Güroy, Güroy, & Soyuturk (2007); Eswaran, Ganesan, Periyasamy, & Rao (2002); Fleurence, Gutbier, Mabeau, & Leray (1994); Fung, Hamid, & Lu (2013); Guiheneuf, Gietl, & Stengel (2018); Hernández, Uriarte, Viana, Westermeier, & Farias (2009); İrkin & Erduğan (2014); Jensen (1963); Jiang, Gong, Lou, and Zou (2019); Kanazawa et al. (2008); Kolb et al. (2004); Lunde(1970); MacArtain, Gill, Brooks, Campbell, & Rowland (2007); Machado, Magnusson, Paul, de Nys, and Tomkins (2014); Machado, Kinley, Magnusson, de Nys, and Tomkins (2015); Mæhre, Malde, Eilertsen, & Elvevoll (2014); Maia, Fonseca, Oliveira, Mendonça, & Cabrita (2016); Marsham, Scott, & Tobin (2007); Moroney, O'Grady, O'Doherty, & Kerry (2012); Neveux, Magnusson, Maschmeyer, de Nys, & Paul (2015); Ometto et al. (2018); Okab et al. (2013); Osório et al. (2020); Peña-Rodríguez, Mawhinney, Ricque-Marie, & Cruz-Suárez (2011); Pereira (2011); Quitain, Kai, Sasaki, & Goto (2013); Rodríguez-Bernaldo de Quirós, Castro de Ron, López-Hernández, & Lage-Yusty (2004); Ripol et al. (2018); Ramus, Lemons, & Zimmerman (1977); Rjiba-Ktita, Chermiti, Bodas, France, & López (2017); Roleda, Hanelt, Krabs, & Wiencke (2004); Romarís-Hortas et al. (2011); Rupérez (2002); Rupérez & Saura-Calixto (2001); Sánchez-Machado, Lopez-Cervantes, Lopez-Hernandez, & Paseiro-Losada (2004); Taboada, Millán, & Míguez (2010); Taboada, Millán, & Miguez (2013); Schiener, Black, Stanley, & Green (2015); Schmid and Stengel (2015); Tayyab, Novoa-Garrido, Roleda, Lind, & Weisbjerg (2016); Ventura, Castanon, & McNab (1994); Wahbeh (1997), Wang, Wang, Zhang, & Tseng (2005); Xiao, Si, Yuan, Xu, & Li (2012).

as 0.5 to 1.0% DM (Kolb, Vallorani, Milanović, & Stocchi, 2004; Kolb, Vallorani, & Stocchi, 1999; Makkar et al., 2016). The lipid component is mainly composed by triacylglycerols, phospholipids and glycolipids.

Protein contents may vary widely among taxonomic groups. Brown algae were shown to present lower protein amount, such as 0.6 to 16.1% DM in *Laminaria* sp. (Moroney et al., 2012; Tayyab, Novoa-Garrido, Roleda, Lind, & Weisbjerg, 2016), while red algae have higher protein content, like 24.1–27.1 (Gaillard et al., 2018; Sánchez-Machado, López-Cervantes, López-Hernández, & Paseiro-Losada, 2004) to 44% DM in *Porphyra* sp. (Marsham et al., 2007). However, seaweeds usually present a high-quality protein, particularly red seaweeds (Corino, Modina, Di Giancamillo, Chiapparini, & Rossi, 2019), since they are rich in essential amino acids, with the exception of the sulphur-containing ones (methionine and cysteine) (Mæhre et al., 2014).

Ash content also varies widely, typically from 10 to 50% DM (İrkin & Erduğan, 2014; Ripol et al., 2018; Tayyab et al., 2016). Hence, macroalgae may contain a high mineral content (Mæhre et al., 2014). This is considered a positive trait with a favourable impact in animal feeds (Morais et al., 2020), due to the importance of minerals on many organic functions, such as cellular metabolism (e.g. iodine) and osmotic regulation (e.g. sodium). Besides several elements ubiquitous in many biological matrices, such as sodium, magnesium, potassium and calcium, the mineral component of macroalgae is very often rich in bromine and iodine. These elements are found at much lower levels in other potential sources of feed ingredients. Although the high levels of mineral compounds can contribute to increase the nutritional value of macroalgae, excessive intakes of sodium, iodine and bromine by livestock animals should be avoided through monitoring and labelling of feed products (Morais et al., 2020). Sodium was described to reach concentration of 100 g/kg w/dw in seaweeds, such as *Porphyra* sp. (Biancarosa et al., 2018), and the amount of iodine can range between 50 and 5,000 ppm, on a dry weight basis (w/dw) (Afonso et al., 2018). Additionally, bromine was found at high levels in several seaweed species (up to 816–972 mg/kg w/dw, in brown algae including *Laminaria ochroleuca* and *Osmundea pinnatifida*) (Afonso et al., 2020; Romarís-Hortas et al., 2011). The concern for animal feed that the high amount of these elements represents, demands a deeper comprehension about compound bioavailability and chemical form (i.e. organic or inorganic forms) (Romarís-Hortas et al., 2011).

Also, problems with the absorption of mineral elements may be present, for instance, the linkage of certain cations to anionic polysaccharides (alginate, agar and carrageenan) may reduce availability for absorption in the digestive tract (Kumar, Ganesan, Suresh, & Bhaskar, 2008). Nonetheless, from the nutritional point of view, the sheer high mineral content in macroalgae may solve this problem.

Macroalgae are able to produce all the vitamins synthesized by terrestrial plants, as they perform photosynthesis (Kumar et al., 2008). Thus, seaweeds are a source of water-soluble (B1, B2, B3 and C) and fat-soluble (E and provitamin A) vitamins. Brown (*e.g. Laminaria* sp. and *Ascophillum nodosum*) and green (*e.g. U. lactuca*) algae species can meet vitamin requirements for livestock animals, particularly for vitamins from complex B (B1, B2 and B3) (NRC, 1994; NRC, 2012), although suffering seasonal effects (Corino et al., 2019). Additionally, brown algae *Laminaria* spp., *A. nodosum* and *Fucus* spp., have a high content of vitamins E and C (Corino et al., 2019) and most red algae, as *Palmaria palmata* and *Porphyra tenera*, contain significant contents of vitamins B_1 and B_2 and large amounts of provitamin A (Kumar et al., 2008). One distinctive feature of macroalgae, when compared with terrestrial plants, is their relatively high content of vitamin B_{12} (Nisizawa, 2002). However, vitamins are heat-labile and may be destroyed to a great extent during the processing of raw macroalgal biomass, being particularly vulnerable to degradation during the drying process and ionisation by UV radiation. Alternative drying methods have been proposed to preserve vitamins, as well as extraction systems, such as solvent extraction, to recover them (Wan, Davies, Soler-Vila, Fitzgerald, & Johnson, 2019). Moreover, although the presence of pseudo-forms or certain algal compounds (e.g. polysaccharide) acting as ligands might compromise vitamin bioavailability, to date, that was not demonstrated for farmed animals (Wan et al., 2019).

Regarding carotenoids, macroalgae contain: β-carotene, lutein, violoxanthin, neoxanthin and zeaxanthin in green algae (Chlorophytes); α- and β-carotene, lutein and zeaxanthin in red seaweeds (Rhodophytes); and β-carotene, violoxanthin and fucoxanthin in brown algae (Phaeophytes) (Mikami & Hosokawa, 2013).

The carbohydrate chemical composition and abundance present wide variability among macroalgal species (Pereira, 2016). Nevertheless, it is possible to formulate some carbohydrate general composition patterns as a function of the three main groups of macroalgae. Usual carbohydrates in brown algae comprise cellulose, alginates (β-1,4-D-mannuronic acid and α-1,4-L-guluronic acid) (Haug et al., 1967), fucoidan (sulphated polysaccharides with L-fucose as one of the major monosaccharides) (Berteau & Mulloy, 2003), laminarin (β-1–3-glucan composed by β-1–3-glucose units with some random β-1–6-side chains) (Brown & Gordon, 2005) and mannitol. Dietary fibre is composed mainly by cellulose and insoluble alginates (El-Said & El-Sikaily, 2013). The main reserve polysaccharides in brown algae are laminarin and mannitol (Kolb et al., 1999). Red algae display specific carbohydrates, which include floridian starch (amylopectin-like α-1,4-glucan), the main storage polysaccharide, cellulose, xylan, mannan and sulphated galactan. In addition, this algae group contains sulphur-containing galactans, such as carrageenan, present in their water-soluble fibre fraction (Jiménez-Escrig & Sánchez-Muniz, 2000). In green macroalga species, there are the water-insoluble cellulose, the water-soluble ulvan (a sulphur-containing polysaccharide), sulphated galactans, mannans and, in some species, the alkali-soluble linear xyloglucan and glucuronans at lower amounts (Lahaye & Robic, 2007). The main storage polysaccharide in green algae is starch (Charoensiddhi, Conlon, Franco, & Zhang, 2017). Simple sugars are also present in seaweeds, including sugar alcohols, such as mannitol that is found in some brown alga species at up to 20% w/dw and operates as osmoregulator (Wei, Quarterman, & Jin, 2013).

TABLE 4 Effects of dietary seaweeds incorporation on growth performance of ruminants, pigs, poultry and rabbits

Macroalgae	Level in the diet (% feed, unless otherwise indicated) and experiment duration	Animal and initial weight/age	Main findings[†]	References
Ruminants				
Ascophyllum nodosum (Tasco-Forage™ extract)	3.4 kg/ha (endophyte-infected or non-infected tall fescue) for 5 to 6 months (2 locations) plus 160-day feedlot finishing period (2 periods, 1 year each)	Steers with 230±8 kg and 234±9 kg (period 1), and with 265±5 kg and 250±2 kg (period 2)	Decrease of FCR (feedlot finishing period; 1 location with consistent effect and 1 location with effect only with endophyte-infected tall fescue)	Allen et al. (2001)
Ascophyllum nodosum (Tasco-Forage™ extract)	1.7 or 3.4 kg/ha (endophyte-infected tall fescue) for 26 (period 1) +22 (period 2) days	Wether lambs with 41±5 kg	Increase of weight gain and ADG	Fike et al. (2001)
Ascophyllum nodosum (extract)	3.0 kg/ha (endophyte-infected-treated hay) or 0.944% (1% dry matter) (previously untreated hay) for 34 days (7 days of sampling)	Wether lambs with 40±5 kg	No effect on body weight	Fike et al. (2005)
Ascophyllum nodosum (extract)	0.92% (2% dry matter) for 14 days (d36 to 50, T1; d105 to 119, T2) and for 28 days (d36 to 50 and d105 to 119, T3)	Steers and heifers with 385±4.5 kg and 10-month-old	No effect on final weight, ADG and FCR	Anderson, Blanton, Gleghorn, Kim, & Johnson (2006)
Ascophyllum nodosum (Tasco–14™ extract)	1% for 14 or 28 days, and 2% for 7 or 14 days	Newly weaned lambs with 19±2.2 kg	No effect on ADG, feed intake, FCR, carcass traits and conformation score	Bach, Wang, & McAllister (2008)
Undaria pinnatifida (by-product of roots and stems)	2% dry matter for 6 months	Steers with 619 kg and 22-month-old	Increase of G:F and tendency for increased ADG; decrease of ADFI	Hwang et al. (2014)
Seaweed meal (Marine Resource Centre, Umm Al Qwain, UAE)	1% for 35 days	Lambs with 13.6±0.95 kg and 120-day-old	Increase of FCR and dry matter intake, decrease of ADG (non-significant) and digestive tract fill/slaughter weight; no effect on relative growth of body components	Al-Shorepy, Alhadrami, & Jamali (2001)
Porphyra sp.	9.7% for 6 weeks	Lambs with 32.9±0.3 kg and 5 month-old	Increase of ADG and feed intake compared to control diet; no effect on ADG and decrease of crude protein intake compared to soybean diet	Lind et al. (2020)
Pigs				
Ascophyllum nodosum (extract)	0.5, 1.0 and 2.0% for 28 days (last 14 days challenge with *Salmonella typhimurium*)	Piglets with 7.1 kg and 24 day-old	Increase of ADG, final body weight (mainly 1%) and ADFI (tendency; possibly overestimated); decrease of G:F (2%) (p = 0.05; possibly underestimated)	Turner, Dritz, Higgins, & Minton (2002)
Ascophyllum nodosum (extract)	0.3, 0.6 or 0.9% for 61 days	Grower–finisher pigs with 48.7±2.5 kg	Decrease of carcass weight and ADG (0.3 to 0.9%) and kill-out yield (0.9%); no effect on ADFI and FCR	Gardiner et al. (2008)

(Continues)

TABLE 4 (Continued)

Macroalgae	Level in the diet (% feed, unless otherwise indicated) and experiment duration	Animal and initial weight/age	Main findings[†]	References
Ecklonia cava (leaves, fucoidan-rich alga)	0.05, 0.10 or 0.15% for 14 and 28 days	Weanling pigs with 7.08±0.15 kg	Increase of ADG and no effect on G:F	Choi et al. (2017)
Laminaria digitata	0.116 or 0.186% for 3 months	Piglets with 17±2 kg	Increase of ADG and ADFI and non-significant decrease of FCR	He, Hollwich, & Rambeck (2002)
Laminaria spp. (laminarian and fucoidan extract)	0.036% fucoidan; 0.030% laminarin for 21 days	Newly weaned pigs with 6.4±0.785 kg and 24 day-old	Increase of ADG and G:F (laminarin); no effect on ADFI	McDonnell, Figat, & O'Doherty (2010)
Laminaria digitata (laminarian and fucoidan extract)	0.28% (0.024% fucoidan; 0.030% laminarin) for 25 days	Newly weaned pigs with 7.6±0.9 kg and 24 day-old	Increase of ADG and G:F	O'Doherty, Dillon, Figat, Callan, & Sweeney (2010)
Laminaria spp. (laminarian and fucoidan extract)	Exp. 1: 0.036% fucoidan; 0.030% laminarin for 9 days	Exp. 1: Newly weaned pigs with 6.9±0.44 kg and 24 day-old	Exp. 1: No effect on ADG, ADFI and G:F	Heim et al. (2014)
	Exp. 2: 0.030% laminarin for 32 days	Exp. 2: Newly weaned pigs with 7.0±0.67 kg and 24 day-old	Exp. 2: Increase of ADG and G:F	
Laminaria spp. (laminarian and fucoidan extract)	0.154-0.50% (0.015-0.050% laminarin; 0.012-0.040% fucoidan) from d109 of gestation until weaning (d28) (sows); 0.024% fucoidan and 0.030% laminarin for 126 days (pigs)	Pregnant sows with mean parity of 3.94±1.8; male pigs with 7.85±1.42 kg	Supplementation of sows: increase of ADG (d 28-126), ADFI and body weight of pigs; supplementation of pigs: no effect on growth (d 0–28); increase of ADG (d 28-70), ADFI (d 28-126), body weight (d 70) and FCR (d 70-126)	Draper, Walsh, McDonnell, & O'Doherty (2016)
Laminaria spp. (laminarian and fucoidan extract)	0.018% laminarin and 0.034% fucoidan for 28 days (last 17 days challenge with *S. typhimurium*)	Female pigs with 30.9±3.65 kg	Increase of ADG and slaughter weight, decrease of FCR and ADFI	Bouwhuis et al. (2017a)
Laminaria spp. (laminarian and fucoidan extract)	1g laminarin extract/day from d109 of gestation to 20 days post-weaning (sows) 0.030% laminarin for 26 days (pigs)	Pregnant sows with mean parity of 2.0; male piglets with 5.62±0.282 kg	Increase of ADG, G:F, ADFI and slaughter weight in pigs born to supplemented sows	Bouwhuis, Sweeney, Mukhopadhya, McDonnell, & O'Doherty (2017b)
Seaweed extract (OceanFeed Swine®)	0.5% for 34 days (between 21 and 55 days; monitoring up to 160 days)	Weanling pigs with 5.96±0.02 kg and 21 day-old	Increase of ADG and slaughter weight, decrease of FCR	Ruiz, Gadicke, Andrades, & Cubillos (2018)

(Continues)

TABLE 4 (Continued)

Macroalgae	Level in the diet (% feed, unless otherwise indicated) and experiment duration	Animal and initial weight/age	Main findings[†]	References
Poultry				
Brown algae mix (*Dictyota dichotoma*, *Dictyota indica*, *Iyengaria stellata*, *Jolyna laminariodes*, *Sargassum cervicorne*, *Stoechospermum marginatum*, *Stockeyia indica*, *Padina pavonia*)	10, 20, 30% and 40% for 1 to 6 weeks	Broiler chicks	Increase (10% and 20%) and decrease (30% and 40%) of body weight for up to 5 weeks, but decreased body weight with 20% after 5 weeks	Zahid Ali, & Zahid (2001)
Chondrus crispus (CC) or *Sarcodiotheca gaudichaudii* (SG)	0.5, 1 or 2% for 30 days	Laying hens 67-week-old	No effect on feed intake, body weight and egg production; decrease of FCR (2% both algae); increase of egg yolk weight (1% SG) and egg weight (1% CC)	Kulshreshtha et al. (2014)
Green algae mix (*Ulva intestinalis*, *Ulva lactuca*, *Ulva taeniata*, *Caulerpa taxifolia*, *Codium flabellatum*, *Codium iyengarii*, *Halimeda tuna*, *Bryopsis pennata*, *Caulerpa scalpeliformis*)	10, 20 and 30% for 6 weeks	Broiler chicks	Increase (10%) and decrease (20 and 30%) of body weight	Zahid, Aisha, & Ali (1995)
Gracilariopsis persica	1, 3 or 5% for 12 weeks	Laying quails with 200±20 g and 5-week-old	No effect on feed intake, body weight, FCR and egg weight	Abbaspour, Davood, & Mohammadi-Sangcheshmeh (2015)
Polymannuronate -Brown algae mix (*Laminaria hyperborea*, *Macrocystis pyrifera*, *Lessonia nigrescens*, and *Ascophyllum nodosum*)	0.1, 0.2, 0.3 or 0.4% for 42 days	Male broilers with 43.77±1.29 g and 1 day-old	Increase of ADG and decrease of FCR	Zhu et al. (2015)
Polysiphonis spp.	Exp. 1: 26.4% for 14 days	Exp. 1: Broiler chicks 14-day-old	Exp. 1: Non-significant decrease of feed intake and body weight gain and increase of FCR	El-Deek & Brikaa (2009)
	Exp. 2: 1.5 or 3.0% for 8 weeks	Exp. 2: Ducklings 1-day-old	Exp. 2: No effect on feed intake, body weight and FCR and carcass traits	
Ulva lactuca	1 or 3% for 21 days	Male broiler chicks 12 to 33 day-old	No effect on feed intake, body weight gain, FCR and nutrients retention; increase of dressing percentage and breast muscle yield of carcass	Abudabos et al. (2013)
Ulva prolifera and *Cladophora* sp. (biomass enriched with microelements)	0.0284% Cu, 0.0924% Mn, 0.0966% Zn, 0.0048% Co, 0.0036% Cr for 38 days	Laying hens 30 and 45-week-old	Increase of eggs weight, eggshell thickness and body weight (Zn; 0.0966%) of hens	Michalak et al. (2011)
Undaria pinnatifida or *Hizikia fusiformis* (fermented and non-fermented by-product)	0.5% for 5 weeks	Male broiler chicks with 44.17±0.05 g and 1-day-old	Increase of body weight gain and G:F (d18 to 35 and all period); lower feed intake with fermented than non-fermented algae (d0 to 17); no effect on relative weight of organs; decrease of mortality rate	Choi, Lee, & Oh (2014)

(Continues)

TABLE 4 (Continued)

Macroalgae	Level in the diet (% feed, unless otherwise indicated) and experiment duration	Animal and initial weight/age	Main findings†	References
Ulva rigida	Exp. 1: 10, 20 or 30%	Exp. 1: Male chicks 10 to 20 day-old	Exp. 1: Decrease of weight gain (20 and 30%) and feed intake (non-significant)	Ventura, Castanon, & McNab (1994)
Ulva sp.	5, 15 or 25% for 35 days	Female chicks 53 day-old	Increase of weight gain and feed efficiency (25%; no significance evaluated), no effect on gizzard and liver weights/body weight	Wong & Leung (1979)
Rabbits				
Ulva lactuca (extract)	1 or 2% for 8 weeks (buck rabbits) and for 1 week plus gestation period (doe rabbits)	Buck rabbits with 4.80±0.41 kg and 6-month-old; doe rabbits with 4.84±0.50 kg and 5- to 6-months-old	Decrease of body weight (2%)	Okab et al. (2013)

†FCR, feed conversion ratio; ADG, average daily gain; G:F, gain:feed ratio; ADFI, average daily feed intake.

It should be emphasized that all of these main constituents of the macroalgal biomass vary not only between species, but also with location, season and maturity of the macroalgae (İrkin & Erduğan, 2014). Although the impact of these factors on the contents of macroalgal constituents is often mentioned in the literature a systematic survey of their influence would be essential for a rational utilization of wild macroalgal resources.

5 | APPLICATIONS OF MACROALGAE IN FEED

The nutritional properties and biological activities of macroalgae and their high growth rates make their biomass a potentially useful raw material for feeds and feed ingredients (Gupta & Abu-Ghannam, 2011b). These feeds may be used to nourish farmed fish and shellfish, but also terrestrial animals. Several studies have tested these macroalga-based feeds with different animals and production systems and have assessed various aspects ranging from animal health to meat quality and shelf-life (Moroney, O'Grady, O'Doherty, & Kerry, 2012). The high content of reserve and structural carbohydrates in seaweeds (Bansemer, Qin, Harris, Howarth, & Stone, 2016) potentially represents a very significant source of energy but with differences among the major groups of macroalgae (Offei, Mensah, Thygesen, & Kemausuor, 2018). This may be one of the factors in selecting the most adequate macroalgae for preparation of feeds. However, the information on the digestibility of carbohydrates in macroalgae is very limited (Bansemer et al., 2016).

Regarding terrestrial animals, swine feeds prepared from macroalgae have been investigated (Moroney et al., 2012; O'Doherty, Dillon, Figat, Callan, & Sweeney, 2010). In particular, supplementation of pig diets with laminarin and fucoidan, attained from the brown seaweed *L. digitata*, has previously been shown to enhance growth performance and improve gut health in pigs (O'Doherty et al., 2010). Also, a reduction in lipid oxidation in *longissimus dorsi* steaks (75% of pigs) and, at a greater extent in liver tissue homogenates, was previously found in pigs fed a diet with macroalgal components (Moroney et al., 2012). There are meaningful examples of the utilization of macroalgae in bovine diet. Namely, the by-products of harvesting and processing of the brown macroalgae *Undaria pinnatifida* have been incorporated in the diet of Holstein cows (Hong et al., 2015). These authors concluded that this macroalgal raw material did not compromise ruminal fermentation and animal performance at low levels (up to 4% inclusion in the diet), and may have potential to be used as a safe feed ingredient in dairy cows. Kaladharan (2006) reported more clearly positive effects on dairy cattle, including higher milk production. Regarding poultry diets (Abudabos et al., 2013; Ali & Memon, 2008), macroalgae have been used to enhance animal immune status, decrease microbial load in the digestive tract and improve the quality of poultry meat and eggs. However, examples are not numerous and the incorporation of macroalgal biomass in these diets is usually up to 6% (Makkar et al., 2016), and can cause a decreased poultry growth when fed at more than 10%.

Moreover, macroalgae are natural options for the formulation of feeds suited to fish and shellfish farming. For instance, Valente et al. (2006) compared two different species, the red alga *Gracilaria bursa-pastoris* and the green alga *Ulva rigida*, reporting that *G. bursa-pastoris* and *U. rigida* had no negative effects on European sea bass (*Dicentrarchus labrax*) growth and may be incorporated at up to 10% in the diet. More recently, there has been much development of the IMTA and a particular embodiment of this type of system is composed of farmed fish, sea urchin and a macroalgae. Successful examples have been reported of the combination of gilthead sea bream (*Sparus aurata*), the macroalgivore sea urchin *Paracentrotus lividus* and the green macroalgae *U. lactuca* (Shpigel et al., 2018). These authors reported that the *P. lividus* feeding on *U. lactuca* and the macroalgae itself improved the economic viability of the IMTA system. In addition, the high biofiltration efficiency of the green algae reduced effluent treatment cost, while the *S. aurata* brought in revenues to the aquaculture unity after one year. Another important example of application of macroalgae in shellfish feed is related to the rearing of abalone (*Haliotis* spp.). These animals, when fed cultivated live macroalgae on-farm, have been reported to exhibit improved feeding activity (i.e. feeding stimulant), better health and an enhanced marketability (Bansemer et al., 2016). In this case, green algae, such as *U. rigida*, red algae, such as *Gracilaria cornea* and *Porphyra columbina*, and brown algae, such as *Macrocystis pyrifera*, are among the most used (Hernández, Uriarte, Viana, Westermeier, & Farias, 2009; Viera et al., 2011).

However, it should be remarked that the utilization of macroalgae in animal feeds presents some concerning issues, namely the uptake of metals by macroalgae from the surrounding water (Utomo et al., 2016). The levels of arsenic, mercury, lead, cadmium, aluminium and nickel in dried macroalgal biomass were reported to be substantial due to bioaccumulation of these elements from water (Chen et al., 2018; Morais et al., 2020), with highest concentrations of aluminium (554 mg/kg) and lowest of mercury (0.0370 mg/kg) (Chen et al., 2018). The continuous surveillance of trace elements, like cadmium, lead and mercury, in seaweeds should be performed attending to algae species, origin and season (Biancarosa et al., 2018; Chen et al., 2018). In a study with two hundred and ninety-five macroalgae species, red algae (*Porphyra* sp.) showed higher levels of cadmium (2.2 mg/kg) and nickel (1.642 mg/kg) but lower levels of mercury (0.010 mg/kg) than brown algae (*Laminaria* sp. and *Undaria* sp.) (0.245, 1.123 and 0.055 mg/kg, respectively) (Chen et al., 2018). Nevertheless, the hazard index was shown to be below one, and, thus, the intake of all seaweeds was not associated to a serious deleterious impact on health (Chen et al., 2018). Another study (Biancarosa et al., 2018) compared red and brown algae with green algae for the presence of heavy metals in twenty-one species. Thus, inferior levels of cadmium in green algae (*U. intestinalis*, *U. lactuca* and *Cladophora rupestris*) (0.12 to 0.18 mg/kg) compared with red (up to 3.1 mg/kg in *Porphyra umbilicalis*) and brown algae (up to 2.6 mg/kg in *Alaria esculenta*) were reported. The lead was present at low concentration in both brown and red algae (≤ 0.58 mg/kg), only reaching levels of up to 3.0 mg/kg in *U. intestinalis*. The mercury level was also low in all macroalgae analysed (not detected to 0.04 mg/kg), and, together with lead, did not excide the maximum levels defined by EU legislation for food supplements (0.1 and 3.0 mg/kg food, respectively). The arsenic levels in red and green algae (6.4 to 24 mg/kg) (Biancarosa et al., 2018) were found to be far below the EU recommended level of 40 mg/kg feed (Directive 2002/32/EC). However, brown alga species are known to be large accumulators of arsenic (Morrison, Baumann, & Stengel, 2008; Ratcliff

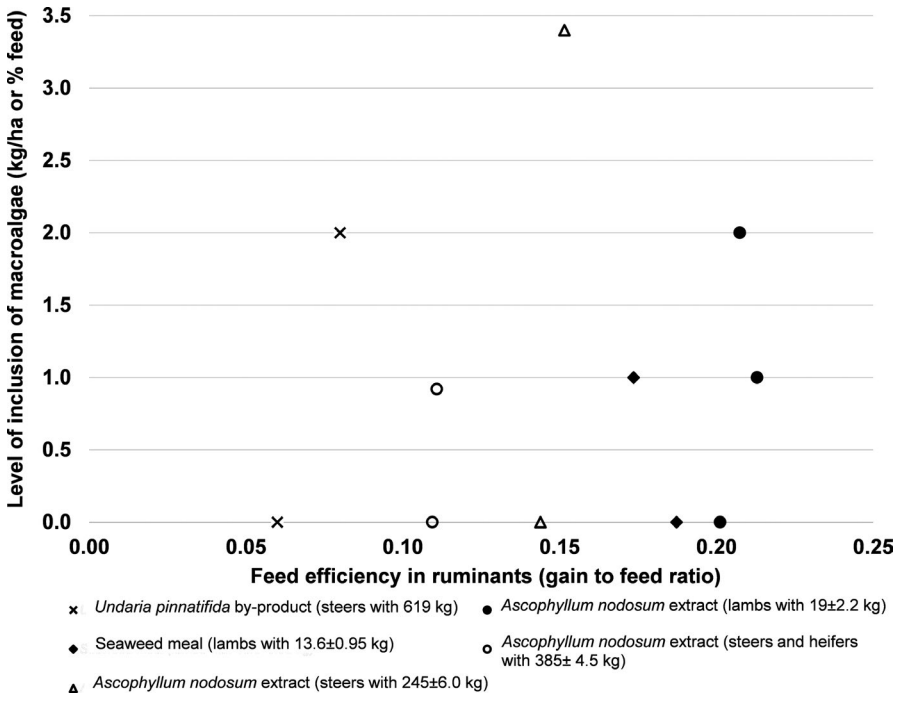

FIGURE 1 Feed efficiency in ruminants fed a diet supplemented with macroalgae between 14 and 183 days. The inclusion levels of *Ascophyllum nodosum extract* fed to 245 kg steers and *Undaria pinnatifida* by-product are expressed in kg/ha and % dry matter, respectively. Data are expressed as mean values. Sources: Allen et al. (2001), Anderson, Blanton, Gleghorn, Kim, & Johnson (2006), Bach, Wang, & McAllister (2008), Al-Shorepy, Alhadrami, & Jamali (2001), Hwang et al. (2014)

TABLE 5 Effects of dietary seaweeds incorporation on meat quality traits of ruminants, pigs and poultry

Macroalgae	Level in the diet (% feed, unless otherwise indicated) and experiment duration	Animal and initial weight/ age	Main findings†	References
Ruminants				
Ascophyllum nodosum (Tasco-Forage™ extract)	3.4 kg/ha (endophyte-infected or non-infected tall fescue) for 5 to 6 months (2 locations) plus 160-day feedlot finishing period (2 periods, 1 year each)	Steers with 230±8 kg and 234±9 kg (period 1) and with 265±5 kg and 250±2 kg (period 2)	Increase of marbling scores and USDA quality grade (more choice and less select frequency)	Allen et al. (2001)
Ascophyllum nodosum (extract)	3.4 kg/ha (endophyte-infected or non-infected tall fescue) for 6 months (2 locations) plus 160-day feedlot finishing period (1 period, 1 year); 7, 14, 21 and 28 post-mortem days and 3 days of retail display	Steers with 265±5 kg and 250±2 kg (2 locations)	No effect on meat sensory characteristics; increase of a* and meat colour uniformity and visual colour scores (day 3 retail display); less meat discoloration and browning scores; increase of cooking loss.	Montgomery et al. (2001)
Ascophyllum nodosum (extract)	3.0 kg/ha (endophyte-infected-treated hay) or 0.944% (1% dry matter) (untreated hay) for 34 days (7 days of sampling)	Wether lambs with 40±5 kg	No effect on meat sensory characteristics; decrease of 18:0 and total SFA and tendency for increase of 14:1 n-5; non-significant increase of 16:1n7, 18:1n9, 18:1n7, 18:2n6 and UFA	Fike et al. (2005)
Ascophyllum nodosum	0.92% (2% dry matter) for 14 days (d 36 to 50, T1; d 105 to 119, T2) and for 28 days (d 36 to 50 and 105 to 119)	Steers and heifers with 385±4.53 kg and 10-month-old	Increase of marbling scores and USDA quality grade (more choice and less select frequency; T1)	Anderson, Blanton, Gleghorn, Kim, & Johnson (2006)
Ascophyllum nodosum (Tasco™ extract)	2% dry matter for 29 days; 10, 17, 24, 31 and 38 *post-mortem* days and 5 days of retail display)	Heifers and steers with 226.8±10.5 kg and 6-month-old	Increase of carcass marbling scores and USDA quality grade (more choice and less select frequency); increase of initial tenderness and decrease of off-flavours; increase of lean a* and *C and decrease of h*, increase of lean colour uniformity (days 1 of retail display) and visual colour scores and decrease of meat discoloration and browning scores; increase of muscle fat and decrease of muscle protein content	Braden et al. (2007)
Seaweed meal (Marine Resource Centre, Umm Al Qwain, UAE)	1% for 35 days	Lambs with 13.6±0.95 kg and 120-day-old	Decrease of non-carcass fat/empty body weight; increase of lean and bone and decrease of fat proportions of rib cut (only non-significant effects)	Al-Shorepy, Alhadrami, & Jamali (2001)
Undaria pinnatifida (by-product of roots and stems)	2% dry matter for 6 months	Steers with 619 kg and 22-month-old	No effect on carcass traits, meat quality grade and muscle chemical composition, except for a decreased cholesterol content; increase of 18:0 and 18:3n-3 and decrease of 14:0, 16:1n-7 and n-6/n-3; tendency for a decrease of PUFA/SFA, no effect on total SFA, UFA and PUFA in the muscle	Hwang et al. (2014)
Pigs				
Laminaria digitata	0.116 or 0.186% for 3 months	Piglets with 17±2 kg	Increase of meat class score (non-significant) and iodine concentration in fresh adipose tissue, muscle, heart, liver and kidneys	He, Hollwich, & Rambeck (2002)

(Continues)

TABLE 5 (Continued)

Macroalgae	Level in the diet (% feed, unless otherwise indicated) and experiment duration	Animal and initial weight/age	Main findings†	References
Laminaria digitata (extract)	0.537 or 2.63% (0.05% laminarin; 0.042% fucoidan) for 21 days; 1, 4, 7, 11 and 14 post-mortem days of storage	Pigs with 14.51 kg	Decrease of muscle TBARS (2.63%); no effect on muscle surface colour, pH and microbial counts	Moroney, O'Grady, O'Doherty, & Kerry (2012)
Laminaria spp. (laminarian and fucoidan extract)	0.045 or 0.090% laminarin plus fucoidan for 3 or 6 weeks; 1, 4, 7, 11 and 14 post-mortem days of storage	Pigs with 82 kg	No effect on muscle pH, colour and 'eating quality' sensory analysis; enhancement of 'visual' sensory analysis by an increase of purchasing appeal and overall visual acceptability (0.045%, 3 weeks); decrease of TBARS (0.045 and 0.090%, 3 weeks) but no effect on DPPH free radical scavenging capacity, SFA (0.090%, 6 weeks) and 18:0 (0.090%, 3 and 6 weeks)	Moroney et al. (2015)
Laminaria spp. (extract)	0.53% (0.018% laminarin and 0.033% fucoidan) for 35 days; 14 post-mortem days of storage	Pigs with 71.1±2.25 kg	Increase of DPPH free radical scavenging capacity and decrease of TBARS and a* (day 4 of storage) and increase of b* (days 7 and 11 of storage)	Rajauria, Draper, McDonnell, & O'Doherty (2016)
Poultry				
Polymannuronate - Brown algae mix (*Laminaria hyperborean*, *Macrocystis pyrifera*, *Lessonia nigrescens* and *Ascophyllum nodosum*)	0.1, 0.2, 0.3 or 0.4% for 42 days	Male broilers with 43.77±1.29 g and 1-day-old	Decrease of TBARS (malondialdehyde, MDA concentration) and increase of glutathione peroxidase (GSH-Px) activity (0.1 and 0.2%)	Zhu et al. (2015)
Ulva lactuca	1 or 3% for 21 days	Male broiler chicks 12- to 33-day-old	Decrease of abdominal fat content and no effect on breast muscle colour	Abudabos et al. (2013)
Ulva sp.	5, 15 or 25% for 35 days	Female chicks 53-day-old	No effect on protein content of pectoral muscle	Wong & Leung (1979)

†USDA, United States Department of Agriculture; SFA, saturated fatty acids; UFA, unsaturated fatty acids; PUFA, polyunsaturated fatty acids; TBARS, thiobarbituric acid reactive substances; DPPH, 2,2-diphenyl-1-picrylhydrazyl.

et al., 2016), with some brown algae (e.g. *L. digitata*, *S. latissima* and *A. esculenta*) showing arsenic levels above 40 mg/kg (Biancarosa et al., 2018). But the majority of arsenic in seaweeds are present in less toxic organic forms, mainly arsenosugars (Biancarosa et al., 2018; Smith, Summers, & Wong, 2010; Taylor et al., 2017), rather than in inorganic forms (Rose et al., 2007). Therefore, it seems that the arsenic threat to the general population as a result of consumption of livestock products reared on a diet consisting of macroalgae-based feed is negligible (Monagail et al., 2018). Monagail et al. (2018) reported that the estimated daily intake of arsenic, for livestock production given a macroalgal feed based on *A. nodosum*, was <0.01% of the suggested safe level. However, the high amount of arsenic inorganic forms in some brown algae, such as *Halidrys siliquosa* (Biancarosa et al., 2018) and *Hizikia fusiforme* (Rose et al., 2007) can have safety implications and hamper their utilization in animal feed.

6 | METHODOLOGY

The research publications reviewed in the present study were all obtained from Web of Science (Clarivate Analytics, Philadelphia, PA, USA) source from 2nd of March to 15th of September of 2020. The values presented in Tables 1, 2 and 3 were converted to the same units of measure. The chemical composition of macroalgae was converted from a wet (w/ww) to a dry (w/dw) weight basis when the % DM or moisture of the algae was available in the report. The individual value of each amino acid (AA) or fatty acid (FA) was obtained, as follows: (AA or FA ×100) / total of AA or FA. In Table 4 and Figure 1, the incorporation level of seaweed extract was converted from % DM to % feed, when the % DM or moisture of the experimental diets was provided. Those converted values are also considered for Table 5.

7 | EFFECTS ON GROWTH PERFORMANCE

The literature review on the influence of dietary macroalgae inclusion on growth performance of ruminant and monogastric species is presented in Table 4. Macroalga cell walls contain a wide variety of complex carbohydrates, such as the polysaccharides alginate, laminarin and fucoidan. The different ability of ruminants and monogastric animals to digest macroalgae cell walls (Makkar et al., 2016) influences the impact of seaweeds on animal growth. Several studies have indicated that macroalgae incorporation in the diet can efficiently improve growth performance in livestock animals, as detailed below.

7.1 | Ruminants

Macroalgae have been used in ruminant animals to improve growth performance. Therefore, seven studies were reviewed where seaweeds were incorporated in diets as either a feed supplement or ingredient. The first consist of extracts of processed whole algae (i.e. *A. nodosum*, Tasco™) (Anderson, Blanton, Gleghorn, Kim, & Johnson, 2006; Allen et al., 2001; Bach, Wang, & McAllister, 2008; Fike et al., 2001, 2005), algal by-product (roots and stems separated during processing of *U. pinnatifida*), or dried and ground seaweed meal collected from fish ponds (Al-Shorepy, Alhadrami, & Jamali, 2001). The latter consist of whole algae that was dried and milled, in order to be used an alternative protein source to soybean meal (i.e. *Porphyra* sp.) (Lind et al., 2020).

Considering macroalgae as an animal feed supplement and extract, *A. nodosum*, which is the most common species of brown alga fed to ruminants (Evans & Critchley, 2014; Makkar et al., 2016), was found to stimulate animal growth (Allen et al., 2001; Fike et al., 2001). The latter results might be due to the use of this macroalgae

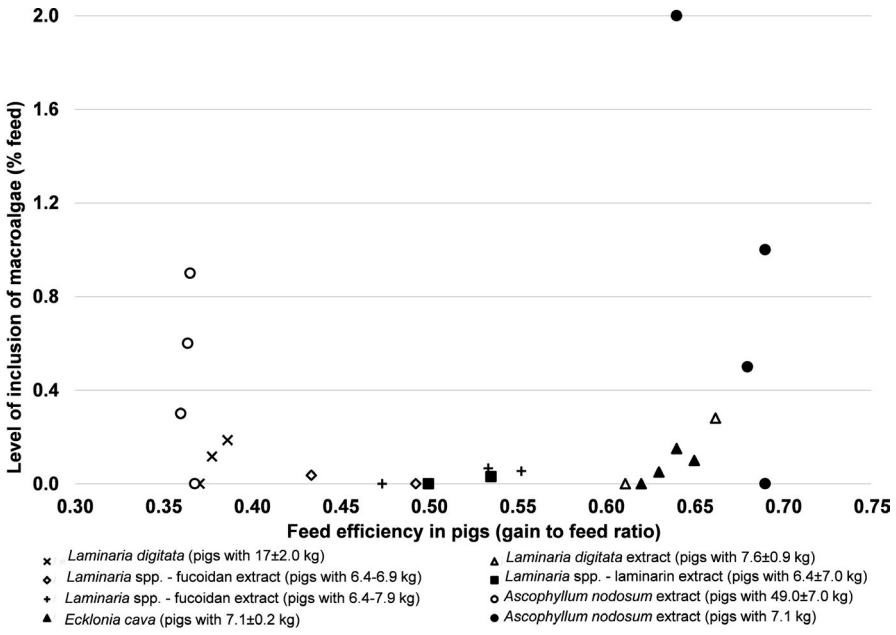

FIGURE 2 Feed efficiency in pigs fed a diet supplemented with macroalgae extracts between 14 and 91 days. The *Laminaria digitata* extract fed to pigs with 7.6 ± 0.9 kg contained 0.024% fucoidan and 0.03% laminarin. Data are expressed as mean values. Sources: Choi et al. (2017), Draper, Walsh, McDonnell, & O'Doherty (2016), Gardiner et al. (2008), He, Hollwich, & Rambeck (2002), Heim et al. (2014), McDonnell, Figat, & O'Doherty (2010), O'Doherty, Dillon, Figat, Callan, & Sweeney (2010), Turner, Dritz, Higgins, & Minton (2002)

as an agent that promotes antioxidant activity in plants and animals (Fike et al., 2001) and acts as an immune-stimulator (Allen et al., 2001). The conteracting of biotic or abiotic stressors by *A. nodosum* was shown in the study of Fike et al. (2001), where wether lambs fed with endophyte-infected fescue pastures treated with *A. nodosum* extract at 1.7 to 3.4 kg/ha had an increased weight gain compared with the animals receiving untreated infected fescue. The absence of stressors renders this brown macroalgae without an effect on ruminant growth. Conversely to Fike et al. (2001), no effect on lambs 'growth was found when algae was incorporated at 1% DM of a hay-based diet (Fike et al., 2005). In addition, no effect on average daily gain (ADG) and gain to feed ratio (G:F) was reported at supplementation rates of 1 to 2% feed in a barley-based diet fed to newly weaned lambs (Bach et al., 2008), or around 0.92% feed (2% DM) in a corn silage-based diet fed to 10 month-old heifers and steers (Anderson et al., 2006). However, an exception was found for steers fed uninfected fescue pastures supplemented with *A. nodosum* extract at 3.4 kg/ha, since the alga supplementation caused a decreased feed conversion ratio (FCR) during the feedlot finishing period, although it was only reported in one of the grazing locations (Allen et al., 2001). Moreover, macroalgae can also be used as a prebiotic agent that modulates gut microbiota. That was described by Bach et al. (2008), which observed a decrease of *Escherichia coli* counts in faeces of steers and lambs fed a barley-based diet supplemented with *A. nodosum* (1 to 2% feed) and, therefore, less bacterial carcass contamination, but without any effect on lamb growth promoted by the algae.

Positive effects on ruminant growth were reported when a by-product of the brown algae *U. pinnatifida* was fed at 2% DM to 22-month-old steers. This alga led to an increased G:F and tended to promote ADG, while decreasing average daily feed intake (ADFI) (Hwang et al., 2014). These results were described to be due to the presence of phlorotannins (Makkar et al., 2016), which can increase the amount of rumen undegradable proteins, thus improving protein utilization in ruminants. The only negative effects of the use of macroalgae as a supplement were reported by Al-Shorepy et al. (2001), since an increase of FCR and DM intake and a non-significant decrease of ADG was found in 120-day-old lambs fed with dried seaweed meal at 1% feed (as is). However, these results were suggested to be caused by the decrease of digestive tract fill due to a laxative effect of that macroalgae mixture.

The dietary incorporation of the red macroalgae *Porphyra* sp. at 9.7% feed (as is) promoted lamb growth. This alga led to an increased ADG and feed intake in 5 months-old lambs, compared with a grass silage and crushed oats-based control diet. Moreover, the lambs fed with either *Porphyra* or soybean diet had similar ADG, showing that *Porphyra* sp. can replace soybean and provide the diet with an identical high-quality protein (Lind et al., 2020). Considering green seaweeds, to date, no effects on growth performance have been reported in ruminants for any specific seaweed.

The relationship between levels of inclusion of macroalgae and G:F in ruminants is presented in Figure 1. The collected data show that this relationship is dependent on the alga species. The incorporation of *U. pinnatifida* by-product at 2% DM in the diet of steers with 619 kg led to an increase of G:F (Hwang et al., 2014), but no significant modification of feed efficiency was observed with *A. nodosum* extract fed at 0.92% feed (2% DM) to steers and heifers with 385 ± 4.5 kg (Anderson et al., 2006), at 3.4 kg/ha to steers with an average of 245 ± 6.0 kg (Allen et al., 2001) or at 1% and 2% feed to newly weaned lambs with 19 ± 2.2 kg (Bach et al., 2008). However, this brown alga extract was shown to influence feed efficiency depending on the location and endophyte-infection of the pasture (Allen et al., 2001). Moreover, a decrease of G:F was found when a seaweed meal was fed at 1% feed to lambs with 13.6 ± 0.95 kg (Al-Shorepy et al., 2001).

7.2 | Pigs

Ten studies were reviewed to analyse the effect of dietary supplements of brown or mixed seaweeds on pig growth performance. Some reports evaluated the use of macroalgae as dried whole algae

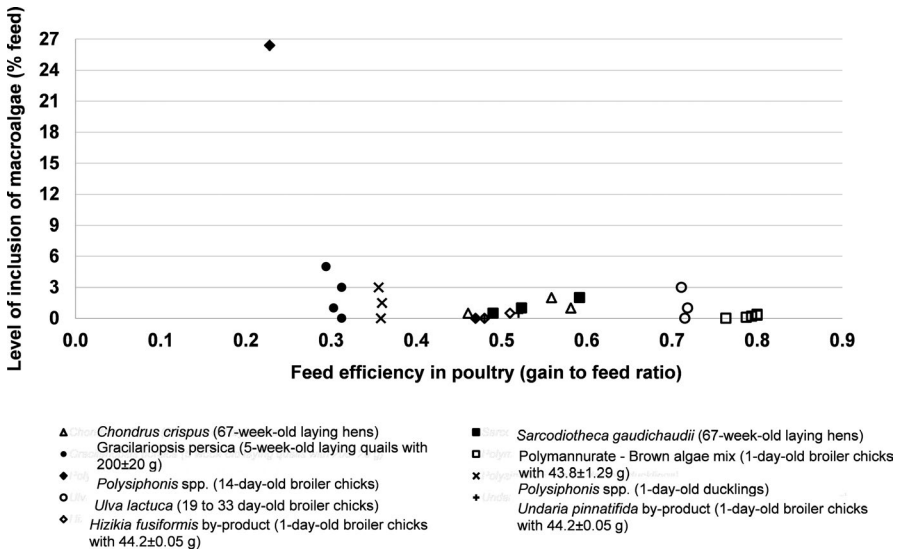

FIGURE 3 Feed efficiency in poultry fed a diet supplemented with macroalgae extracts between 14 and 84 days. Data are expressed as mean values. Sources: Abbaspour, Davood, & Mohammadi-Sangcheshmeh (2015), Abbaspour et al. (2015), Abudabos et al. (2013), Choi, Lee, & Oh (2014), El-Deek and Brikaa (2009), Kulshreshtha et al. (2014), Zhu et al. (2015)

(He, Hollwich, & Rambeck, 2002) (*L. digitata* and *Laminaria hyperborea*), dried and ground algal leaves (Choi et al. 2017) (*Ecklonia cava*), processed whole algae extract (i.e. *A. nodosum*) (Gardiner et al., 2008; Turner, Dritz, Higgins, & Minton, 2002) or brown, red and green algae mixed extract (Ruiz, Gadicke, Andrades, & Cubillos, 2018). However, the majority of studies added extracted polysaccharides (i.e. laminarin and/or fucoidan) from brown seaweeds (i.e. *Laminaria* sp.) to pig diet (Bouwhuis, et al., 2017a; Bouwhuis, Sweeney, Mukhopadhya, McDonnell, & O'Doherty, 2017b; Draper, Walsh, McDonnell, & O'Doherty, 2016; Heim et al., 2014; McDonnell, Figat, & O'Doherty, 2010; O'Doherty et al., 2010). These compounds were used due to their prebiotic, antimicrobial, antioxidant, anti-inflammatory and immune-stimulant properties (Corino et al., 2019), which can be important in the stressful post-weaning period where pigs are exposed to infection by gut bacteria (e.g. *Salmonella typhimurium*) (Bouwhuis, et al., 2017a, b). Therefore, with the exception of two studies that only reported the effects of macroalgae on grower and finisher pigs (Bouwhuis, et al., 2017a; Gardiner et al., 2008), all studies described the effects of macroalgae on weanling pigs. Ruiz et al. (2018) and Draper et al., (2016) reported the long-term effects of algae, from weaning to slaughter. In some reports, seaweed compounds were fed to piglets and lactating sows, in order to see the repercussion on offspring growth (Bouwhuis, et al., 2017b, Draper et al., 2016). Although algae extracts were used to replace cereals, such as cornstarch (Turner et al., 2002) and wheat (Gardiner et al., 2008), low amounts of algae were incorporated (up to 1 to 2% feed), which consequently conferred algae compounds a supplement rather than an ingredient function.

The dietary supplementation with whole *Laminaria* spp. at 0.116 and 0.186% feed (as is) (He et al., 2002) or *E. cava* algae leaves at 0.05 to 0.15% feed (as is) (Choi et al., 2017) were shown to increase ADG in piglets. The effect of *Laminaria* spp. was suggested to be due to a high bioavailability of iodine from this alga and, thus, an enhancement of pig´s basal metabolism with consequently increased protein synthesis (He et al., 2002). The fact that algae leaves were rich in fucoidan that was responsible for an increase of ileal villous height (Choi et al., 2017) and, thus, nutrient absorption, might explain the stimulation of piglet growth.

On the other hand, the dietary supplementation with algae extract led to inconsistent results on pig growth. *A. nodosum* extract was shown to increase ADG and final body weight when fed to newly weaned pigs at 0.5 to 1% feed (Turner et al., 2002), whereas, a decreased ADG was found when this brown alga was fed to grower-finisher pigs at 0.3 to 0.9% feed (Gardiner et al., 2008). The health status (*e.g. S. typhimurium*-infected pigs in the first study versus uninfected pigs in the second study) and growth stage of the pigs may be factors affecting the effectiveness of *A. nodosum*. Overall, these results showed that positive effects on growth could be found, when algae extracts were given to weanling pigs. However, its influence might only be detected in latter stages of growth with pigs processing a mature immune system (Corino et al., 2019). In fact, Ruiz et al. (2018) described an increased ADG and G:F in fattening pigs (up to 160 days) when a seaweed mixture extract was fed, at nursery period (24 to 55 days of age), at 0.5% feed (processed). The stimulation of growth was associated with prebiotic and anti-microbial activity of algae compounds demonstrated by decreased *E. coli* and increased *Lactobacillus* counts in faeces (Ruiz et al., 2018).

The addition of extracted polysaccharides, such as laminarin at 0.030% feed (Heim et al., 2014; McDonnell et al., 2010), or a mixture of laminarin at 0.018 (Bouwhuis, et al., 2017a) to 0.030% (O'Doherty et al., 2010) feed and fucoidan at 0.024% (O'Doherty et al., 2010) to 0.034% (Bouwhuis, et al., 2017a) feed, was shown to increase ADG and G:F in newly weaned or grower pigs. Only a decrease of G:F was reported by Draper et al. (2016) when the same mixture of laminarin and fucoidan was added to piglet diet. In one study (Bouwhuis, et al., 2017b), the stimulation of pig growth was reported in pigs born to laminarin extract supplemented sows (1 g/day). These results were previously described to be due to enhanced gene expression of nutrient transporters in the ileum (Heim et al., 2014), as well as an increased number of *Lactobacillus* spp. and a decreased number of coliforms (*E. coli*) (O'Doherty et al., 2010) and other *Enterobactereaceae* (Lynch, Sweeney, Callan, O'Sullivan, & O'Doherty, 2010) in the pig gut. Additionally, laminarin and fucoidan extracts were able to increase duodenal villous height (Walsh, Sweeney, O'Shea, Doyle, & O'Doherty, 2013) and 'villous height: crypt depth' ratio (Walsh et al., 2013). Furthermore, the anti-inflammatory effect of algal polysaccharides with consequent reduction of pro-cytokines (e.g. interleukins) (Bouwhuis, et al., 2017a, b) might have contributed to reduce energy and amino acidic expenditure (Corino et al., 2019) and, thus, promote pig growth.

The relationship between the level of macroalga inclusion and G:F in pigs is presented in Figure 2. The collected data show that this relationship is dependent on the algae species, the development stage of the pig and the bioactivity of the polysaccharides present in the seaweed. No significant modification of feed efficiency was observed when *A. nodosum* was fed at 0.3 to 0.9% feed to pigs with 48.7 ± 2.5 kg (Gardiner et al., 2008) or at 0.5 to 2% feed to pigs with 7.1 kg (Turner et al., 2002). In the latter study, the decrease ($p = 0.05$) of G:F with 2% of alga inclusion was possibly underestimated by feed wastage (Turner et al., 2002). Also, *E. cava* fed at 0.05 to 0.15% feed caused no significant effect on G:F, although a slight numerical increase (from 0.62 to 0.65) was observed at inclusion levels of up to 0.10% (Choi et al., 2017). Conversely, the dietary incorporation of *Laminaria* spp. influenced feed efficiency in piglets but with inconsistent results. An increase of G:F (from 0.50 to 0.54) was found in pigs with 6.4 to 7 kg fed laminarin extract at 0.03% feed, but no significant effect on feed efficiency was reported when pigs were fed fucoidan extract at 0.036% feed (Heim et al., 2014; McDonnell et al., 2010). Moreover, a decrease, or a tendency for a reduction, of G:F was reported in pigs with 7.85 ± 1.42 kg fed both laminarin (0.03% feed) and fucoidan (0.024% feed) at 70 to 126 days or 28 to 126 days after weaning, respectively (Draper et al., 2016). Conversely, others found that the combination of the two polysaccharides caused either a non-significant numerical increase (from 0.47 to 0.53) of G:F in pigs with an average of 6.65 ± 0.61 kg (Heim et al., 2014; McDonnell et al., 2010), or a significant increase of G:F in pigs with

7.6 ± 0.9 kg fed *L. digitata* extract at 0.28% feed (O'Doherty et al., 2010). Similarly, an enhancement of feed efficiency was found in older piglets with 17 ± 2.0 kg fed 0.116 to 0.186% of *L. digitata* (He et al., 2002).

7.3 | Poultry

Twelve studies were reviewed to analyse the effect of macroalgae on poultry growth, when incorporated as a feed supplement or ingredient. The first consist of whole brown algae by-products (fermented or non-fermented) (i.e. *U. pinnatifida* and *H. fusiformis*) (Choi, Lee, & Oh, 2014); purified polymannuronate obtained by processing of alginate that was extracted from a brown algae mixture (i.e. *L. hyperborean*, *M. pyrifera*, *Lessonia nigrescens* and *A. nodosum*) (Zhu et al., 2015). Additionally, dried and ground whole red algae (*Polysiphonia* spp., El-Deek & Brikaa (2009); *Chondrus crispus* and *Sarcodiotheca gaudichaudii*, Kulshreshtha et al. (2014)) were used, respectively, as pellet binder or prebiotic; and also fresh whole green seaweeds (i.e. *Ulva prolifera*, former *Enteromorpha prolifera*, and *Cladophora* sp.) for microelements supplementation (Michalak et al., 2011).

The latter consist of a brown whole air-dried and ground algae mixture (eight species, among which *Sargassum cervicorne*; Zahid Ali, & Zahid (2001)); whole dried and ground green seaweeds (*U. rigida*, *Ulva taeniata*, *U. lactuca* or *Ulva* sp.) (Ventura, Castanon, & McNab, 1994; Zahid, Aisha, & Ali, 1995; Abudabos et al., 2013; Wong & Leung, 1979) used to replace basal dietary ingredients, such as corn (Abudabos et al., 2013); or whole red algae processed in a similar way and replacing soybean meal and corn (*G. persica* and *U. lactuca*) (Abbaspour, Davood, & Mohammadi-Sangcheshmeh, 2015) or just soybean meal (*Polysiphonia* spp.) (El-Deek & Brikaa, 2009) as protein and amino acid source.

Considering macroalgae as an animal feed supplement, brown algae by-products were shown to increase body weight gain and G:F, when fed at 0.5% feed to broilers (Choi, et al., 2014). These findings were associated to an activation of humoral immune response (i.e. increase of IgA and IgM), showing the importance of seaweed compounds as immunomodulators. Similar results were found when purified polymannuronate, which is a polymer of (1–4) linked β-D-mannuronic acid that is part of alginate, was fed to chicks at up to 0.4% feed (Zhu et al., 2015). The low molecular weight polymers caused an increase of ADG and G:F due to their prebiotic activity (i.e. modification of caecal bacterial diversity with increase of lactic acid bacteria and decrease of *E. coli*), alteration of gut fermentation (i.e. increased concentrations of lactic and acetic acids in caecum), immunomodulatory (i.e. increase of Ig M) and antioxidant properties (Zhu et al., 2015).

However, inconsistent results on poultry growth have been described in the literature with red macroalgae. Indeed, no significant effect on growth was observed when *Polysiphonia* spp. was fed at 1.5 and 3% feed (as is) to 1-day-old ducks (El-Deek & Brikaa, 2009). Conversely, *C. crispus* and *S. gaudichaudii* fed to 67-week-old laying hens at 1 or 2% feed (as is) led to a decrease of FCR and increase of egg weight (Kulshreshtha et al., 2014). The latter results were likely due to a modification of ileal microbiota (i.e. increase of transcripts of *Bifidobacterium longum* and *Streptococcus salivarius*, decrease of transcripts of *Clostridium perfringens*), caecal fermentation and an increase of ileal villus height and surface area and, thus, promoted nutrient absorption (Kulshreshtha et al., 2014).

The use of green macroalgae highlights their application as organic mineral feed additives for replacement of inorganic ones (Makkar et al., 2016). *U. prolifera* and *Cladophora* sp. were shown to increase body weight, egg weight and eggshell thickness in laying hens fed algal biomass (0.0966% to 0.0036% feed, as is) enriched with microelements, with emphasis for zinc, cobalt and copper (Michalak et al., 2011). These results were likely due to a higher bioavailability of minerals in organic than in inorganic forms (Makkar et al., 2016).

Macroalgae used as feed ingredient for poultry caused distinct effects depending on the level of incorporation. For instance, a brown algae mixture, including *S. cervicorne* (Zahid et al., 2001), led to a decreased final body weight in broiler chicks fed the algae at 20% and 30% feed (as is), whereas, 10% of inclusion caused an opposite effect. Similar results were found with *U. rigida* (Ventura et al., 1994) or a green algae mixture containing species from *Ulva* genus (Zahid et al., 1995) fed to chicks at levels between 10 and 30% feed (as is), although *U. rigida* caused a variable effect on weight gain instead of body weight. Ventura et al. (1994) even suggested that the dietary inclusion of macroalgae as a feed ingredient for 10 to 20-day-old chicks should be limited to 10% feed due to the high content of indigestible polysaccharides present in seaweeds. However, when the level of alga incorporation was too low, no significant effect on broiler chick growth was reported (Abudabos et al., 2013). For instance, *U. lactuca* fed at up to 3% feed (as is) to 12 to 33-day-old chicks led to only a numerical increase of body weight gain and increased dressing percentage and breast muscle yield of carcass (Abudabos et al., 2013). These slight effects were probably due to an enhancement of crude protein content and essential amino acids, such as threonine and methionine, in the algal diets, which contradicts the low sulphur-essential amino acids content of *U. lactuca* described by Mæhre et al. (2014). Differences on seaweed protein quality might be caused by distinct seasonal and geographical conditions. Additionally, it is essential to consider the growth stage of the chicks when choosing the appropriate level of inclusion of green algae. *Ulva* sp. was shown to cause a non-significant increase of weight gain and feed efficiency when fed to older broiler chicks (53-day-old) at 25% feed (as is) (Wong & Leung, 1979).

The dietary inclusion of the red macroalgae *G. persica* and *Polysiphonia* spp. did not impair poultry growth, when fed to 14-day-old broiler chicks at 26.4% feed (as is) (El-Deek & Brikaa, 2009) or to 5 week-old laying quails at 1 to 5% feed (as is) (Abbaspour et al., 2015), respectively. These results evidenced the high-quality of protein presented in seaweeds, making them a valuable ingredient for replacement of other protein sources, such as soybean meal.

The relationship between the level of inclusion of macroalgae and G:F in poultry is presented in Figure 3. The collected data show

that this relationship was dependent on algae and animal species. Both *G. persica* and *U. lactuca* had no effect on feed efficiency when fed at 1 to 5% feed to 5-week-old laying quails with 200 ± 20 g (Abbaspour et al., 2015) or at 1 to 3% feed to 19 to 33-day-old broiler chicks (Abudabos et al., 2013), respectively. Similar results were found when *Polysiphonis* spp. was fed at 1.5 to 3% feed to 1-day-old ducklings, but higher inclusion rates (26.4% feed) of the same seaweed fed to 14-day-old broiler chicks led to a decrease of G:F (from 0.47 to 0.23) (El-Deek & Brikaa, 2009). In contrast, feeding either 67-week-old laying hens with *C. crispus* or *S. gaudichaudii* at 0.5 to 2% feed or 1-day-old broiler chicks (average of 43.97 ± 0.67 g) with *U. pinnatifida*, *H. fusiformis* by-products (Choi et al., 2014) and a purified polymannuronate from a brown algae mix (Zhu et al., 2015) at 0.4 to 0.5% feed led to an increase of feed efficiency.

7.4 | Rabbits

The effect of a feed supplement (1 to 2% feed) of green seaweed *U. lactuca* on the growth of 6-month-old buck rabbits and 5 to 6-months-old doe rabbits was evaluated and a decrease of final body weight was reported with the alga at 2% feed (Okab et al., 2013). The authors suggested that this result was probably due to low digestible nutrients (i.e. polysaccharides) and high ash contents of alga, with the consequent reduction of palatability and feed intake, even though the latter variable was not analysed in the study.

8 | EFFECTS ON MEAT QUALITY

The bibliographic review concerning the influence of dietary macroalgae inclusion on meat quality of ruminant and monogastric species is shown on Table 5. Overall, macroalgae are rich in n-6 and n-3 PUFA (Cardoso et al., 2017; Kendel et al., 2015; Wahbeh, 1997), which would contribute to have a healthier meat product for consumers. In addition, seaweeds were shown to have important antioxidant potentials due to their high contents in polyphenols (*e.g.* phlorotannins) (Makkar et al., 2016), α-tocopherol, carotenoids and ascorbic acid (Plaza et al., 2008), thus contributing to enhance meat shelf-life. Several studies have demonstrated that dietary macroalgae inclusion can efficiently improve meat quality in livestock animals, as detailed below.

8.1 | Ruminants

The processed extract of the brown macroalgae *A. nodosum* (Tasco^{TM}) is the only feed supplement presently reviewed, as it was used to increase meat quality in six studies. This seaweed was shown to increase carcass marbling scores (i.e. intramuscular fat deposition) and USDA quality grade when fed to 10- (Anderson et al., 2006) and 6-month-old (Braden et al., 2007) steers and heifers at 2% DM and to grazing steers at 3.4 kg/ha (Allen et al., 2001). These results might be related to immune-stimulating properties (*e.g.* increase of monocyte phagocyte activity and major histocompatibility complex class II expression) of *A. nodosum* extract, described, for instance, in steers grazing infected fescue treated with 3.4 kg extract/ha (Saker et al., 2001) and, thus, less energy spent for immune system function and more for fat deposition. Also, an increase of a* value (more redness) and meat visual colour and colour uniformity scores, as well as a decrease of meat discoloration and browning scores, were reported when this macroalga extract was fed to 6-month-old (Braden et al., 2007) steers and heifers at 2% DM and to grazing steers at 3.4 kg/ha (Montgomery et al., 2001). These effects of alga were suggested to be due to its antioxidant activity, causing, for instance, an increased amount of oxymyoglobin (oxygenated myoglobin) and a decreased amount of metmyoglobin (brown, oxidized myoglobin) in finished-ruminants (up to 170 days) fed with algae extract at 2% DM (Braden et al., 2007).

Moreover, *A. nodosum* processed extract was shown to have antioxidant activity by increasing superoxide dismutase in fescue and serum concentration of vitamin E and vitamin A in wether lambs grazing endophyte-infected fescue foliarly applied with 1.7 to 3.4 kg extract/ha, even though the amount of serum vitamin E was decreased with uninfected treated-fescue (Fike et al., 2001). Additionally, the concentration of vitamin E tended to be enhanced in the liver of steers grazing both infected and uninfected fescue treated with extract at 3.4 kg/ha (Montgomery et al., 2001).

Overall, no major impact of *A. nodosum* extract was found on meat sensory traits when it was fed to wether lambs at 3.0 kg/ha or 1% DM (Fike et al., 2005) or to steers at 3.4 kg/ha (Montgomery et al., 2001), although increased initial tenderness and decreased off-flavours were reported when steers were fed the extract at 2% DM (Braden et al., 2007).

The influence of macroalgae on meat FA composition was evaluated for wether lambs fed *A. nodosum* extract at 3.0 kg/ha or 1% DM, and a decrease of 18:0 and total SFA and a non-significant increase of unsaturated fatty acids (UFA) (i.e. 14:1n-5; 16:1n-7, 18:1n-9, 18:1n-7, 18:2n-6) were observed for both inclusion levels (Fike et al., 2005).

8.2 | Pigs

The brown algae *Laminaria* spp. has been widely used as a feed supplement to increase meat quality in pigs, either in the form of dried whole algae (He et al., 2002) or polysaccharides (i.e. laminarin and fucoidan)-based seaweed extracts (Moroney et al., 2012; Moroney et al., 2015; Rajauria, Draper, McDonnell, & O'Doherty, 2016), as reviewed in a total of four studies. The whole alga *L. digitata* led to a non-significant increase of meat score and to an enhancement of iodine concentration in fresh adipose tissue and muscle in piglets fed the alga at 0.116 or 0.186% feed (as is). As described for growth, these results were caused by a higher bioavailability of iodine in organic than in inorganic form (Makkar et al., 2016). Laminarian and fucoidan extracts from processed algae were shown to exert antioxidant activity in muscle. In fact, a decreased lipid peroxidation

(TBARS assay) was found when pigs were fed a wet form of *L. digitata* extract at 2.63% feed, providing laminarin at 0.05% feed and fucoidan at 0.042% feed (Moroney et al., 2012). Similar results were reported with the same extracted algae species but delivering diets with total laminarin and fucoidan concentration of either 0.045% feed or 0.090% feed (Moroney et al., 2015). Additionally, *Laminaria* spp. extract at 0.53% feed (0.018% laminarin and 0.033% fucoidan) were shown to cause both a decrease of lipid peroxidation and an increased DPPH free radical scavenging capacity (Rajauria et al., 2016). However, no effect of the seaweeds on DPPH inhibition was reported by Moroney et al. (2015), which might have been due to a biotransformation of laminarin and fucoidan into unreactive compounds.

The decrease of a* and increase of b* values on surface of fresh *longissimus dorsi* muscle after feeding pigs with polysaccharides-based *Laminaria* spp. extract, in the study of Rajauria et al. (2016), was suggested to be caused by an interaction between the mixture of laminarin (0.018% feed) and fucoidan (0.033% feed) and meat constituents. Moroney, O'Grady, O'Doherty, & Kerry (2013) showed that one of the constituents might be muscle oxymyoglobin, and meat surface redness can be a function of extract´s concentration.

Moreover, feeding pigs with laminarin and fucoidan extract at 0.045% feed for 3 weeks was shown to have a positive effect on visual sensory analysis, with an increase of purchasing appeal and overall visual acceptability of meat stored up to 7 days.

The influence of macroalgae on pork FA composition was evaluated for pigs fed laminarin and fucoidan extract at 0.045 or 0.090% feed. Thus, a decrease of 18:0 and total SFA was observed with extract at 0.090%, which indicated the beneficial effect of these algal polysaccharides on muscle FA profile (Moroney et al., 2015).

8.3 | Poultry

Seaweeds have been used in poultry as feed supplement or ingredient to improve meat quality, which was reviewed in three studies. The first consist of a purified polymannuronate that was a compound of alginate extracted from a brown algae mixture (Zhu et al., 2015), whereas the latter was whole dried and ground green algae from *Ulva* genus (*Ulva* sp. and *U. lactuca*) (Wong & Leung, 1979; Abudabos et al., 2013).

The polymannuronate supplementation caused a linear reduction of lipid peroxidation in breast muscle (TBARS assay) when fed at increasing amounts 0.1 to 0.4% feed (processed) to 1-day-old broilers chicks. The antioxidant activity of this alginate polymer was reinforced by an increased glutathione peroxidase activity (GSH-Px) with polymannuronate at 0.1 and 0.2% feed (Zhu et al., 2015). Other studies have also reported that alginate oligomers and polymers can exert strong antioxidant activities (Tomida et al., 2010; Zhao, Li, Xue, & Sun, 2012), which might contribute to an increased meat shelf-life.

Few meat-quality parameters were analysed when *Ulva* genus was fed to chicks as a dietary ingredient. Thus, the amount of abdominal fat, breast colour (Abudabos et al., 2013) and protein content of pectoral muscle (Wong & Leung, 1979) were assessed. The only parameter that was influenced by algae feeding was the amount of abdominal fat, which gradually decreased when *U. lactuca* was fed at 1 and 3% feed (as is) to 12 to 33-day-old broiler chicks (Abudabos et al., 2013). The latter authors suggested that these data could be explained by an increase of dietary soluble fibre and consequent enhance of viscosity, bile salt binding capacity and fermentability (Davidson & McDonald, 1998).

9 | CONCLUSIONS AND FUTURE PERSPECTIVES

The most common algae feed supplements are brown macroalgae extracts, such as *A. nodosum* for ruminants at up to 2% DM and *Laminaria* sp. extracted polysaccharides (fucoidan and laminarin) for pigs at up to 0.04% feed, each. In addition, the main algae feed ingredients are green seaweeds, such as *Ulva* sp., for poultry at a recommended level of dietary incorporation of up to 10% feed. The reviewed literature showed that all these seaweeds could improve growth performance and meat quality in livestock animals. These results were attributed to the high nutritional quality of algae and to immunomodulatory, prebiotic and antioxidant properties of algae compounds (*e.g.* bioactive polysaccharides). Besides the advantageous of using macroalgae in animal nutrition, seaweeds are expected to contribute to global climate change mitigation, which is of relevance to environmental sustainability.

However, feeding macroalgae is also associated to potential constraints, which include an excessive bioaccumulation of inorganic elements from seawater (*e.g.* iodine) and heavy metals, such as arsenic, mercury, lead, cadmium and aluminium. There may also exist problems of nutritional quality due to nutrient loss (e.g. vitamins), as a result of macroalgal processing for incorporation in animal feeds, an inferior content of protein compared with soybean meal and digestibility problems (i.e. algal recalcitrant cell walls). In addition, some relevant challenges can be found related to algal production, such as the costs of large-scale production (*e.g.* nutrient resources), harvesting and drying of macroalgae. Thus, the environmental impacts may be significant as revealed by LCA, especially due to macroalgal drying, if no countervailing measures are taken. Regardless of all these constraints of feeding and producing seaweeds, many of them can be irrelevant or minimized. The current levels of metals in seaweeds were not associated to a serious deleterious impact on health. The nutritional quality problems can be minimized through preservation of vitamins with alternative drying methods and extraction systems. Additionally, the lower amount of protein in algae is overcome by its high quality, and the dietary application of specific CAZymes can enable the degradation of algae cell wall polysaccharides with consequent increase of nutrients bioavailability. Moreover, the use of IMTA, which may represent a sustainable and profitable system for algae production, and the application of low energy and natural alternatives of algal drying can countervail the environmental impacts of producing macroalgae.

Overall, the positive effects of seaweed feeding on animal growth and meat quality, as well as their contribution to environmental sustainability, can make algae a promising alternative to staple food crops, such as corn and soybean, as feed ingredients. This aspect would allow a reduction of the growing competition between food and feed chains.

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CONFLICT OF INTEREST STATEMENT

The authors confirm that this work involves no conflict of interest.

ANIMAL WELFARE STATEMENT

The authors confirm that the ethical policies of the journal, as noted on the journal's author guidelines page, have been adhered to. No ethical approval was required as this is a review article with no original research data.

DATA AVAILABILITY STATEMENT

Data sharing is not applicable to this article as no new data were created or analysed in this study.

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