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Review article

Seaweeds for livestock diets: A review☆

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ABSTRACT

Seaweeds are macroalgae, which generally reside in the littoral zone and can be of many different shapes, sizes, colours and composition. They include brown algae (Phaeophyceae), red algae (Rhodophyceae) and green algae (Chlorophyceae). Seaweeds have a long history of use as livestock feed. They have a highly variable composition, depending on the species, time of collection and habitat, and on external conditions such as water temperature, light intensity and nutrient concentration in water. They may contain non-protein nitrogen, resulting in an overestimation of their protein content, and nitrogen-to-protein conversion factors lower than 6.25, normally used for feed ingredients, have been advocated. They contain considerable amount of water. Most essential amino acids are deficient in seaweeds except the sulphur containing amino acids. Seaweeds concentrate minerals from seawater and contain 10–20 times the minerals of land plants. They contain only small amounts of lipids (1–5%), but majority of those lipids are polyunsaturated n-3 and n-6 fatty acids. Brown seaweeds have been more studied and are more exploited than other algae types for their use in animal feeding because of their large size and ease of harvesting. Brown algae are of lesser nutritional value than red and green algae, due to their lower protein content (up to approx. 14%) and higher mineral content; however brown algae contain a number of bioactive compounds. Red seaweeds are rich in crude protein (up to 50%) and green seaweeds also contain good protein content (up to 30%). Seaweeds contain a number of complex carbohydrates and polysaccharides. Brown algae contain alginates, sulphated fucose-containing polymers and laminarin; red algae contain agars, carrageenans, xylans, sulphated galactans and porphyrans; and green algae contain xylans and sulphated galactans. In ruminants, step-wise increase in the levels of seaweeds in the diet may enable rumen microbes to adapt and thus enhance energy availability from these complex carbohydrates. In monogastrics, those polysaccharides may impact the nutritional value but the addition of enzyme cocktails might help. *In vivo* studies on ruminants, pigs, poultry and rabbits reveal that some seaweeds have the potential to contribute to the protein and energy requirements of livestock, while others contain a number of bioactive compounds, which could be used as prebiotic for enhancing production and health status of both monogastric and ruminant livestock. Seaweeds tend to accumulate heavy metals (arsenic), iodine and

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other minerals, and feeding such seaweeds could deteriorate animal and human health. Regular monitoring of minerals in seaweeds would prevent toxic and other undesirable situations.

Contents

1. Introduction

Algae are a heterogeneous group of plants with a complex and often controversial taxonomy. There are two main types of algae: macroalgae (seaweeds), which occupy the littoral zone and can be of very large size; and microalgae, the small-sized algae, which are found in benthic and littoral habitats as well as throughout the ocean waters as phytoplankton (Hasan and Chakrabarti, 2009; El Gamal, 2012). There are about 10,000 species of seaweeds (Guiry, 2014), but only a few of them are of interest for animal feeding. Some common names of seaweeds are macroalgae, marine macroalgae and kelp in English; algues and algues marines in French; and algas and algas marinas in Spanish. The main genera and species used as animal feed are given in Table 1.

Seaweeds have been used to feed livestock for thousands of years and have been mentioned in Ancient Greece and in the Icelandic sagas. In Iceland, where long periods of fodder scarcity are common, seaweeds were grazed by sheep on the beaches, or fed to sheep, horses and cattle for 6–8 weeks of the year, and up to 18 weeks in some cases. Seaweeds were dried and stored in barns, and there are reports of seaweeds being preserved as silage and used as winter feedstuff for sheep and

Table 1
Main genera and species of seaweeds used as animal feed.

Genera and species	Common name
Ascophyllum nodosum	Rockweed, Yellow tang, Norwegian kelp, Knotted kelp, Knotted wrack and Egg wrack in English; Goémon noir, Algue noueuse, Robert, Favach and Ascophylle noueuse in French
Laminaria species	Kelp, Tangle and Devil's apron in English; Laminaire in French
Lithothamnion species	Rhodoliths, Maerl in English; Maërl in French
Macrocystis pyrifera	Giant kelp, Giant bladder kelp in English; Sargazo gigante, Huiro, Cochayuyo, Cachiyuyo and Chascón in Spanish (Mexico)
Sargassum species	Sargassum in English; Sargasse in French; Sargazo in Spanish
Palmaria palmata	Dulse, Dillisk, Dilsk, Red Dulse, Sea lettuce flakes, Creathnach in English; Goémon à vache, Algue à vache and Petit goémon in French
Ulva species	Sea lettuce in English; Laitue de mer in French

cattle in the early 1900s (Evans and Critchley, 2014). In the 19th and early 20th centuries, there were numerous reports of occasional or systematic use of seaweeds to feed livestock in France (Brittany), the Scottish islands and Scandinavia (Gotland, Norway, Finland), mostly to ruminants (including calves) and pigs (Sauvageau, 1920; Chapman and Chapman, 1980). Today, the Orkney sheep in the North Ronaldsay Islands (Northern Scotland) still graze a diet almost exclusively based on seaweeds (Hansen et al., 2003). Wild white-tailed deers have been observed grazing seaweeds in coastal Maine (USA) (Applegate and Gray, 1995). During World War I, feed shortages led to a "considerable exaggeration" of the nutritional value of seaweeds (Chapman and Chapman, 1980). In Germany, it was shown that pigs, cows, ducks and sheep could eat a seaweed meal for many months as an additional food and thrive as well as control animals fed on a conventional diet (Beckmann, 1915 and 1916, cited by Chapman and Chapman, 1980). In 1917, the French army carried out several promising experiments on feeding horses with *Laminaria*, *Saccharina* and *Fucus* (Sauvageau, 1920). However, in the first half of the 20th century, the general consensus, based on nutrition science, had become that seaweeds were of too poor nutritive value to be recommended for livestock (Evans and Critchley, 2014).

Seaweeds have seen a renewed interest as feed ingredients since the 1960s, when Norway started producing seaweed meal from kelp (after a first attempt in 1939–1941) (Naylor, 1976; McHugh, 2002). Seaweeds are valuable alternative feeds for livestock, mostly as sources of valuable nutricines, notably chelated micro-minerals, the availability of which is higher than that of inorganic ones; complex carbohydrates with prebiotic activities; and pigments and polyunsaturated fatty acids beneficial to consumer health (Evans and Critchley, 2014; CEVA, 2005). Soluble *Ascophyllum nodosum* extracts obtained from alkaline hydrolysis are used as feed additives (Allen et al., 2001a,b; Williams et al., 2009). Seaweeds are used as binding agents in shrimp feeds (CEVA, 2005). In addition to use in livestock feed, seaweeds have a number of other uses (see Section 3).

Seaweeds contain considerable amount of water. This review presents characteristics, chemical composition and nutritional attributes of seaweeds on dry matter basis, and constraints in their use in terrestrial animal feed. Conclusions drawn and way forward are also presented. To our knowledge, hitherto, no such synthesis is available. It is expected that this state-of-the-knowledge review will open new avenues for investigations leading to accelerated developments in fully exploiting potential of this neglected unconventional resource for the feed industry. Given that the world would need between 60% and 70% more animal products in 2050 than it consumes today, the livestock agriculture would need a large amount of feed, which would be a big challenge given the scenarios of increase in land degradation, food-fuel-feed competition, population and water deprivation and of on-going climate change. Enlargement of feed resource base through identification of novel feeds or development of new additives that enhance resource use efficiency would play a vital role in sustainable development of the livestock sector.

2. Seaweed species

Seaweeds include brown algae (Phaeophyceae), red algae (Rhodophyceae) and green algae (Chlorophyceae) (Chapman and Chapman, 1980; El Gamal, 2012). They are of many different shapes, sizes, colours and composition and occupy various habitats. Some species remain attached to rocks or other supporting material, and some are attached to the ocean floor through root like structures (holdfasts) whereas other species float on the water surface and form single or multi-celled colonies (Murty and Banerjee, 2012). The term "seaweed" does not have any taxonomic value, but is rather a popular term used to describe the common large marine algae.

2.1. Brown algae

Brown algae live primarily in shallow waters or on shoreline rocks and have very flexible stems that allow them to withstand the constant pounding of the waves (Ghosh et al., 2012). Due to their larger size and ease of harvesting, brown seaweeds have been more studied and are more exploited than other algae types for their use in animal feeding. Brown algae are the largest seaweeds, up to 35–45 m in length for some species and extremely variable in shape. The most common genera include *Ascophyllum*, *Laminaria*, *Saccharina*, *Macrocystis*, *Nereocystis*, and *Sargassum* (Murty and Banerjee, 2012).

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Ascophyllum nodosum (L.) Le Jolis has long, leathery fronds (up to 2 m long) with characteristic ovoid air-bladders. It occurs in the mid-littoral zone in wave-sheltered rock shores of the northern Atlantic, from the Artic shores to Portugal and New Jersey. *A. nodosum* is harvested in Europe (Norway, Ireland, France and Iceland) and Canada for alginate, feed and fertilizer production (Edwards et al., 2012; Guiry and Guiry, 2014; Guiry, 2014; Evans and Critchley, 2014).

Laminaria and *Saccharina* (notably *Laminaria digitata* (Hudson) J. V. Lamouroux, *Laminaria hyperborea* (Gunnerus) Foslie and *Saccharina latissima* (L.) C. E. Lane, C. Mayes, Druehl & G. W. Saunders) are characterized by their long (1.5 m) and smooth laminated blades. These algae form extensive beds, mainly in cold-temperate waters of the north Pacific and in the Atlantic. They occur on rocky shores at low tide and in the subtidal zone to depths of 8–30 m, though some species occur at depths of up to 120 m in the Mediterranean and in South-Western Atlantic. *Laminaria* and *Saccharina* have a long history of use in animal feeding in Western and Northern Europe (Sauvageau, 1920) and are still of great economic importance. They are harvested in Europe and Asia for alginate, food and feed production (Edwards et al., 2012; Guiry and Guiry, 2014; Guiry, 2014).

Macrocystis pyrifera (L.) C. Agardh, commonly known as giant kelp, has very large fronds that can reach 50 m or more. It is distributed mainly in the southern hemisphere (South America, Southern Africa, Australia and New Zealand) and in the Northeast Pacific coast. It occurs in the shallow part of the tidal zone, and it can be found at depths of up to 40 m. When it can anchor itself to rocky bottom areas, *M. pyrifera* forms extensive "kelp forests" that are home to many marine species. It has a very fast growth rate, from 14 to 23 cm/d. *M. pyrifera* is harvested for the production of alginate, animal feeds and pharmaceutical additives (Cruz-Suarez et al., 2008).

Sargassum are found in temperate, subtropical and tropical waters around the globe. They are of variable size, even within the same species. For example *Sargassum muticum* (Yendo) Fensholt is 1–2 m long in its native Japanese waters but can reach 16 m in Brittany, France. *Sargassum* species live in a wide range of habitats, and many species have the ability to become free-floating and form large floating mats in open waters (Casas-Valdez et al., 2006; Guiry, 2014).

2.2. Red algae

Red algae have a characteristic bright pink colour caused by biloprotein pigments (R-phycoerythrin and R-phycocyanin). Most marine red algae species occur from low tide marks to 100 m depth. Major red algae genera include *Pyropia*, *Porphyra*, *Chondrus* and *Palmaria*.

Pyropia and *Porphyra* species are red algae with smooth, thin fronds that grow in the intertidal zone of temperate oceans. They are the largest source of food from red seaweeds – *Pyropia tenera* (Kjellman) N. Kikuchi & M. Miyata, M.S. Hwang & H.G. Choi (formerly *Porphyra tenera*) is used in Japanese sushi, for instance – and they are cultivated on a large scale in Japan, China and South Korea (McHugh, 2003).

Palmaria palmata (L.) Weber & Mohr has smooth leathery fronts, deep red in autumn and greenish/yellow in summer. Individuals can grow up to 30–40 cm. This species occurs in the North Atlantic and is found in moderately exposed to exposed shores and in areas subjected to tidal currents. It is rich in protein and harvested for food (Edwards et al., 2012). In the 19th and early 20th centuries, *P. palmata* was eaten by sheep and goats in Gotland (Sweden) and by cows in Brittany (France) (Sauvageau, 1920).

Coralline red algae, especially *Phymatolithon* and *Lithothamnion*, are shaped as small nodules that secrete calcium carbonate. Dead coralline algae form calcareous deposits called maerl that are exploited all around the world as a source of calcium carbonate (Edwards et al., 2012). Maerl extracts (under the name of calcified seaweed extracts) are used to create ruminal buffers (Melo and Moura, 2009; Montanez-Valdez et al., 2012).

2.3. Green algae

Green algae are typically green in colour due to the presence of chlorophyll in their chloroplasts. Their overall colouration depends on the balance between these chlorophylls and other pigments such as beta-carotene and xanthophylls. Main genera include *Ulva*, *Codium*, *Enteromorpha*, *Chaetomorpha* and *Cladophora*. Green algae are common in areas where light is abundant, such as shallow waters and tide pools.

Ulva species are commonly known as sea lettuce, due to their thin and bright green fronds. *Ulva lactuca*, also called water lettuce, is the most studied among *Ulva* species. There are other species of *Ulva* that are similar and difficult to differentiate. They can grow up to 45 cm and occur worldwide in the intertidal zone of brackish or marine environments, particularly in estuaries (Edwards et al., 2012). Ulvoids, which include *Ulva* and related genera (*Enteromorpha*, *Chaetomorpha*, *Cladophora*, *Rhizoclonium*, *Percursaria*, *Ulvaria*) are fast-growing algae. Optimal environmental conditions (temperature, concentration in nutriments) can cause algal blooms called "green tides" that are a major environmental issue in several countries, notably in China, Japan and France (Yabe et al., 2008). All *Ulva* species are edible (Edwards et al., 2012).

3. Uses

Seaweeds have many uses. They are consumed as food in several cultures, notably in Asia. In Japan, the red seaweed nori (*Pyropia* and *Porphyra*), is a traditional wrapping for sushi and is eaten in soups. Wakame (*Undaria pinnatifida*) and kombu (*Saccharina japonica*) are cultivated for food (Hasan and Chakrabarti, 2009). Seaweeds are used in medicine for

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the treatment of iodine deficiency (goitre, Basedow's disease and hyperthyroidism), for intestinal disorders, as vermifuges, and as hypocholesterolemic and hypoglycemic agents (El Gamal, 2012). They provide numerous ingredients to the food or pharmaceutical industries such as hydrocolloids (agar-agar, alginates used as stabilizers, thickeners and fillers), pigments, vitamins, chelated micro-minerals (selenium, chromium, nickel, arsenic) and prebiotic substances in the form of complex carbohydrates (alginates, fucose-containing polymers, mannitol and laminarin) and phlorotannins (Evans and Critchley, 2014). Seaweeds (particularly brown and red algae) are used as organic fertilizers that are usually rich in potassium but poor in nitrogen and phosphorus (Waaland, 1981 cited by Abdel-Raouf et al., 2012). Seaweed species such as *Gracilaria* (red algae) and *Ulva* (green algae) are suitable for bioremediation. Seaweeds are used in integrated aquaculture systems (Troell et al., 2009).

Seaweeds for food are usually cultivated in Asia while they are harvested in the wild in Europe. The main species cultivated for food are *Saccharina japonica* (Japanese kelp), *Euchema* species, *Gracilaria* species, *Pyropia* and *Porphyra* (nori), *U. pinnatifida* (wakame). Other species such as *Sargassum fusiforme* and *Caulerpa* spp. are farmed in small quantities (FAO, 2012). Seaweed meal is produced by drying and milling, and several commercial products exist in Europe, Asia and North America. It is difficult to have a clear picture of the current state of macroalgae utilization in animal feeding. It seems that seaweed meal and extracts obtained from *A. nodosum* in Norway and the UK, *L. digitata* in France, *Ascophyllum* and *Laminaria* species in Iceland provide the main commercial ingredients used to feed land animals (McHugh, 2002).

In integrated fish farming systems, seaweeds can remove up to 90% of the nutrient discharge from an intensive fish farm. Seaweed cultivation could alleviate eutrophication problems due to aquaculture or to wastewater discharges (Lüning and Shaojun Pang, 2003; Merrill, 1996). They are also good substrates for generating biogas (Herrmann et al., 2015).

4. Seaweed cultivation, harvest and meal production

The culture of seaweed is a growing worldwide industry. Driven by the development of fish farming, seaweed production increased yearly by 9.5% during the 1990s and by 7.4% yearly during the 2000s, from 3.8 million tonnes in 1990 to 19 million tonnes in 2010 (FAO, 2012). In 2012, seaweed production resulted from cultivation (>95%) rather than from collection, the main producers being China, Japan and Indonesia (FAO, 2012).

Seaweeds develop under variable environments. Every species has its own requirements for water salinity, nutrients, water movement, temperature and light. In species that propagate vegetatively, seaweed pieces are tied to ropes or nets or sunk at the bottom of the pond, unattached or held in place by a fork-shaped tool (in sediments) or sand-filled tubes (in sandy soil). Such species are harvested either by removing the entire plant or by removing most of it but small pieces that are used as seedstock for further cultivation. In brown seaweeds, which mainly reproduce sexually, only the large sporophyte form is harvested (McHugh, 2003). This FAO publication (FAO, 2012) can be referred to for details on seaweed culture and production.

For seaweed meal production, seaweeds once harvested must be rapidly handled because they are rich in water and can become mouldy. The wet seaweed is passed through hammer mills with progressively smaller screens in order to reduce it to fine particles. It is then dried in a drum-dryer starting at 700–800 °C and exiting at no more than 70 °C. Seaweed meal should have a final moisture level of about 15% and should be stored in sealed bags. Seaweed meal can be stored for about a year (McHugh, 2003). Because seaweeds contain a number of phytochemicals, low temperature drying is suggested. Low temperature drying and storage would allow least inactivation of the bioactive compounds.

5. Nutritional attributes

Seaweeds have a highly variable composition, with large differences in the final content in proteins, minerals, lipids and fibre (Table 3), which depends on the species, time of collection and habitat, and on external conditions such as water temperature, light intensity and nutrient concentration in water (Mišurcová, 2012). One common feature of fresh seaweeds is that they contain very large amounts of water (70–90%) and need to be consumed quickly or dried.

Brown algae are of lesser nutritional value than red and green algae, due to their lower protein content and higher mineral content; however brown algae contain a number of bioactive compounds.

Algae may contain non-protein nitrogen (such as free nitrates), resulting in an overestimation of their protein content. Nitrogen-to-protein conversion factors of 5.38, 4.92 and 5.13 for brown, red and green algae respectively have been proposed (Guiry, 2014; Mišurcová, 2012). Some seaweeds such as the brown seaweed *U. pinnatifida* and the red seaweed *P. palmata* and have been reported to have valuable amino acid profiles for human nutrition. Their essential aminoacid index (EAAI) are close to standard protein: EAAI of red seaweed *P. palmata* was 103.7% of the standard protein for humans and EAAI of brown seaweed *U. pinnatifida* was 95.9% of the standard protein. Both seaweeds can thus be considered high-value proteins for humans (Dawczynski et al., 2007). Among the essential amino acids (Table 2) sulphur containing amino acids need special mentioning. The methionine *plus* cystine values (expressed in g/16 g nitrogen) in *M. pyrifera* and *Ulva* species were substantially higher than those in soymeal. This makes these two seaweeds a good feed for wool producing animals, and also high sulphur amino acid content renders them good candidates for overcoming toxicity because methyl donors are required to detoxify toxic constituents in the liver, which could be provided by these amino acids. Methionine level in *A. nodosum* is comparable with soybean protein. Lysine levels in the three seaweeds reported in Table 2 are lower than those in soymeal. The levels of phenylalanine *plus* tyrosine were lower in *A. nodosum* and *Ulva* species than in soymeal, while the

Table 2
Amino acid composition (g/16 g nitrogen) of seaweeds *versus* soymeal.

Amino acids	*Ascophyllum nodosum*	*Undaria pinnatifida*	*Saccharina japonica*	*Macrocystis pyrifera*	*Ulva* sp.	Soymeal
Essential						
Methionine	1.3 (0.7–1.9)	1.9 (1.7–2.2)	1.7 (0.9–2.4)	1.9 ± 0.4 (5)	1.6 (1.3–1.9)	1.32
Cystine	Not available	1.2 (0.9–1.5)	2.2 (1.2–3.2)	2.6 ± 0.9 (4)	5.9	1.38
Valine	4.1 (3.7–4.4)	7.8 (5.2–10.3)	6.7 (3.8–9.7)	5.2 ± 1.7 (6)	4.4 (4.2–4.5)	4.5
Isoleucine	3.1 (2.8–3.4)	4.5 (4.1–4.9)	3.5 (2.7–4.2)	3.4 ± 0.2 (5)	2.6 (2.2–2.9)	4.16
Leucine	5.3 (4.6–6.0)	7.9 (7.4–8.4)	6 (4.9–7.2)	5.8 ± 0.4 (5)	5.2 (5.0–5.3)	7.58
Phenylalanine	3.2 (2.3–4.0)	4.7 (4.7–4.8)	3.9 (3.2–4.5)	3.8 ± 0.4 (5)	3.6 (3.4–3.8)	5.16
Tyrosine	0.9	2.8 (2.6–2.9)	2.3 (1.7–2.8)	2.6 ± 0.2 (4)	1.4	3.35
Histidine	1.4 (1.3–1.5)	2.9 (2.5–3.2)	3 (2.2–3.8)	1.3 ± 0.3 (4)	2.0 (1.6–2.3)	3.06
Lysine	4.6 (4.3–4.9)	6.2 (5.6–6.8)	5.8 (3.9–7.7)	4.7 ± 0.7 (5)	3.8 (3.7–3.9)	6.18
Threonine	3.6 (2.8–4.3)	4.4 (4.4–4.5)	4.5 (3.5–5.5)	4.6 ± 0.6 (5)	3.8	3.78
Tryptophan	Not available	0.5 (0.3–0.7)	0.4 (0.3–0.5)	0.9 ± 0.1 (4)	Not available	1.36
Non-essential						
Serine	3.5 (3.0–4.0)	3.8 (3.5–4)	3.6 (3.3–4)	4.2 ± 0.6 (5)	4.2 (3.8–4.6)	5.18
Arginine	6.0 (4.0–8.0)	5.2 (5.2–5.2)	4 (3.3–4.8)	3.5 ± 0.7 (5)	4.5 (3.2–5.7)	7.64
Glutamic acid	11.6 (10.0–13.1)	10.5 (6.5–14.5)	15 (6.2–23.8)	14.3 ± 2.4 (5)	13.3 (11.0–15.5)	19.92
Aspartic acid	8.4 (6.9–9.8)	7.5 (6.2–8.7)	10 (7.6–12.5)	9.7 ± 1.1 (5)	7.9 (7.3–8.4)	14.14
Proline	3.0 (2.6–3.4)	3.5 (3.4–3.6)	3.1 (3.1–3.1)	3.6 ± 0.2 (5)	2.8	5.99
Glycine	4.8 (4.5–5.0)	5.2 (5.1–5.4)	4.7 (4–5.3)	4.5 ± 1.0 (5)	5.4 (4.9–5.9)	4.52
Alanine	5.4 (5.3–5.4)	10.7 (4.7–16.7)	6.5 (5.7–7.3)	10.9 ± 1.8 (5)	5.9 (5.5–6.2)	4.54

Sources: Anderson et al. (2006), Arieli et al. (1993), Castro-Gonzalez et al. (1994), Cruz-Suarez et al. (2008), Dawczynski et al. (2007), Gojon-Baez et al. (1998), Kolb et al. (2004), Ortiz et al. (2009).
Values are mean ± SD (*n*); other values are either single or average of two values, each value given in bracket.

levels of these amino acids in *M. pyrifera* were lower than in soymeal. Arginine is considered as an essential amino acids for poultry which was lower in the three seaweeds (Table 2). It can be surmised that most essential amino acids are deficient in seaweeds except the sulphur containing amino acids. However, the amino acid composition among seaweeds of the same species was found to be highly variable (Mišurcová, 2012). For instance, a study on *P. palmata* found that some amino acids such as lysine, disappeared during certain months of the year (Galland-Irmouli et al., 1999).

Marine macroalgae concentrate minerals from seawater and contain 10–20 times the minerals of land plants (Moreda-Piñeiro et al., 2012). They are thus a significant source of valuable minerals for nutrition (Mišurcová, 2012). Brown seaweeds, and particularly *Laminaria*, accumulate iodine and the coralline red seaweeds such as *Lithothamnion*, once dead, form exploitable sources of calcium carbonate.

Seaweeds contain only small amounts of lipids (1–5% DM), but majority of those lipids are polyunsaturated n-3 and n-6 fatty acids. Lipids of brown and red seaweeds contain predominantly 20:5 n-3 (EPA) and 20:4 n-6 (arachidonic acid). The lipids of brown seaweed *Durvillaea antarctica* and green seaweed *U. lactuca* contained 73% and 52% of unsaturated fatty acids respectively (Mišurcová, 2012), while those of red seaweed *Gracilaria changgi* contained 75% of polyunsaturated fatty acids (33% EPA) and palmitic acid was the main saturated fatty acid with 26% (Norziah and Ching, 2000).

Chemical composition (as % in dry matter, DM) of brown, red and green seaweeds is discussed below (see Table 3). This table gives data for only those seaweeds for which more than 2 values are available in literature. For others the values are mentioned in the text.

5.1. *Brown seaweeds*

Brown seaweeds are rich in minerals (14–35% DM) and contain low to moderate amounts of crude protein (5–12% for *A. nodosum*, 8–13% DM for *Laminaria and Saccharina*, 7–13% for *M. pyrifera*, 6–11% for *Sargassum*) (Table 3). An early study on *L. digitata* and *Saccharina japonica* in Scotland also found large seasonal differences in composition: crude protein varied from a maximum of 12–14% DM in spring to a minimum of 4–8% in autumn (Black, 1950). Cell walls are made of cellulose and alginic acid, a long-chained heteropolysaccharide that is present in large quantities (15–30% for *A. nodosum*, 20–45% for *L. digitata*, 20–27% for *M. pyrifera*) (Rodríguez-Montesinos and Hernández-Carmonal, 1991; Guiry, 2014). The cell walls of several of brown seaweeds, particularly of Fucales and Laminariales, consist mainly of fucoidans, which are composed of variable amounts of saccharide units with different degree of sulphation (Mišurcová, 2012). The principal carbohydrate reserve in brown seaweeds is laminarin (also called laminaran), a polysaccharide of glucose, unlike other seaweeds in which starch is the storage carbohydrate. The brown colour results from the dominance of the xanthophyll pigment fucoxanthin, which masks the chlorophylls, beta-carotene and other xanthophylls (Guiry, 2014).

Brown seaweeds are rich in potassium (2–3% in *A. nodosum*, 1.3–3.8% in *L. digitata*), sodium (3–4% in *A. nodosum*, 0.9–2.2% in *L. digitata*) and particularly iodine (up to 0.1% in *A. nodosum* and 1.1% in *L. digitata*) (Rodríguez-Montesinos and Hernández-Carmonal, 1991; Guiry, 2014). Indeed, *Laminaria* have the capacity to accumulate iodine by more than 30,000 times the iodine concentration in the seawater (Mišurcová, 2012). The composition varies according to different factors. For instance, *M. pyrifera* harvested during summer in the coast of Mexico has higher amounts of minerals and amino acids than that harvested

Table 3
Chemical composition of seaweed species (all values on DM basis).

Analysis	*Ascophyllum nodosum*	*Macrocystis pyrifera*	*Laminaria* and *Saccharina* sp.	*Sargassum* sp.	*Palmaria palmata*	Maerl deposits	*Ulva* sp.
Crude protein (%)	8 ± 2.7 (5)	10.1 ± 2.3 (7)	9.8 ± 2.2 (49)	8.5 ± 1.8 (10)	19.1 ± 6.1 (12)	NA	18.6 ± 7.3 (14)
Crude fibre (%)	5.5 (4.1–6.8)	8 ± 2.5 (5)	6.6 (5.5–7.7)	10.1 ± 2.4 (9)	1.5	NA	6.9 ± 4.1 (7)
NDF (%)	20.9 (19.8–22.0)	19.9	16.6	29.5 ± 3.4 (5)	NA	NA	26.2 ± 5.4 (6)
ADF (%)	13.1	12.6	NA	21.3 ± 4.4 (4)	NA	NA	8.7 ± 6.2 (4)
Lignin[a] (%)	13.8 (6.2–21.4)	3.6		4.5 (1.0–7.9)	NA	NA	3.5 ± 2.1 (3)
Ether extract (%)	3.9 ± 1.6 (3)	0.6 ± 0.2 (7)	0.8 (0.5–1.0)	1.2 ± 0.9 (9)	NA	NA	1.2 ± 0.8 (14)
Ash (%)	22.5 ± 2.1 (12)	32 ± 9.5 (7)	31.5 ± 7.5 (79)	35.9 ± 12.8 (9)	24.5 (17.5–31.5)	95 ± 0.8 (5)	23 ± 7.4 (13)
Gross energy (MJ/kg)	14.6 (14.5–14.7)	9 ± 0.4 (5)	NA	9.1 (8.9–9.2)	NA	NA	14.7 ± 2.6 (4)
Ca (g/kg)	20	14.1 ± 1.5 (3)	8.8	3.8 ± 2.6 (4)	NA	335.9 ± 11.2 (61)	29.2 ± 28.9 (3)
P (g/kg)	1	2.9 (2.6–3.2)	3	2.2 ± 1 (5)	NA	NA	2.7 ± 2.1 (3)
K (g/kg)	24	67.5 ± 22.4 (3)	59.5	46.2 (15.9–76.6)	NA	NA	22.1 (15.1–29.0)
Na (g/kg)	NA	36.9 ± 9.9 (3)	25.3		NA	3.3 ± 0.3 (51)	20.2 (11.0–29.3)
Mg (g/kg)	8	39 ± 22.8 (3)	5.5	7.7 (7.5–7.9)	NA	32.7 (32.2–33.2)	16.7 ± 3.2 (3)
Mn (mg/kg)	12 ± 3 (8)	11	6 ± 2 (12)	214 ± 106 (4)	11	NA	101
Zn (mg/kg)	181 ± 114 (8)	12	111 ± 70 (12)	214 ± 151 (5)	143	NA	45 (28–61)
Cu (mg/kg)	28 ± 16 (1)	2	14 ± 9 (12)	7 ± 4 (5)	24	NA	12 (7–17)
Fe (mg/kg)	134 ± 36 (8)	117	233 ± 233 (12)	7291 ± 6327 (5)	153	NA	1246 (1052–1440)

Sources: Abudabos et al. (2013), AFZ (2011), Anderson et al. (2006), Applegate and Gray (1995), Arieli et al. (1993), Bindu and Sobha (2004), Black (1950), Casas-Valdez et al. (2006), Castro et al. (1991), Castro-Gonzalez et al. (1994), Cruz-Suarez et al. (2008), Dawczynski et al. (2007), Dierick et al. (2009), Diler et al. (2007), El-Deek and Al-Harthi (2009), Erickson et al. (2012), Galland-Irmouli et al. (1999), Gojon-Baez et al. (1998), Gowda et al. (2004), Kolb et al. (2004), Kut Guroy et al. (2007), Lunde (1970), Marín et al. (2009), Marsham et al. (2007), Mišurcová et al. (2010), Mora-Castro et al. (2009), Okab et al. (2013), Ortiz et al. (2009), Rai et al. (2008), Rupérez and Saura-Calixto (2001), Sebahattin et al. (2009), Valente et al. (2006), Ventura et al. (1994), Ventura and Castanon (1998), Zitouni et al. (2014).

Values are mean ± SD (n); other values are either single or average of two values, each value given in bracket.

[a] Lignin values reported in the tables were obtained by different methods.

NA, not available.

during winter (Castro-Gonzalez et al., 1994; Rodríguez-Montesinos and Hernández-Carmonal, 1991). *A. nodosum* contains high amounts of phenolic compounds (phlorotannins) that are insoluble in the digestive tract of animals (McHugh, 2003; Wang et al., 2008). One specific aspect of many seaweeds is their high content in free glutamic acid (Table 2), which gives the "*umami*" taste characteristic of the Japanese cuisine and which is used as a palatability enhancer in human food (Yamaguchi and Ninomiya, 2000). *Sargassum* are poor in protein but are good source of carbohydrates and of readily available minerals (Gojon-Baez et al., 1998; Marín et al., 2009). They are rich in beta-carotene and vitamins and do not contain antinutritional factors (Casas-Valdez et al., 2006).

5.2. Red seaweeds

Red seaweeds tend to be rich in protein, with a 10–29% DM range reported for *P. palmata* (Galland-Irmouli et al., 1999; Mišurcová et al., 2010); whereas, protein values in the 18–50% DM range have been reported for *Porphyra* and *Pyropia* species, Table 3 (Davies et al., 1997; Marsham et al., 2007; Mišurcová et al., 2010; Rupérez and Saura-Calixto, 2001). It may be noted that these two seaweeds are currently largely used as food. Unlike brown seaweeds, red algae contain limited amounts of iodine (0.03–0.04%), though still in higher concentrations than in other plants (Mišurcová, 2012). The main storage polysaccharide of red seaweeds is the floridean starch, a polysaccharide close to starch that does not contain amylose. Cell walls of red algae are made of carrageenans and agars, which are phycocolloids of high industrial importance. They also contain cellulose, though in much more limited amounts than in higher plants; particularly, *P. palmata* is very poor in cellulose and *Porphyra*/*Pyropia* species contain insoluble mannan and xylan rather than cellulose (Mišurcová, 2012). *P. palmata* is rich in some minerals (Na, K, Cl) and to a lesser extent in Ca, Fe and Mg (Table 3). It contains lipids in low levels (0.3–3.8%), but the fatty acid profile shows that it is rich in C22:6 n-3 (DHA) and EPA (Morgan et al., 1980). In *P. palmata* harvested in the French Atlantic coast, a seasonal effect due to the sun exposition was observed on the nitrogen content, which was highest in winter and early spring, at the expense of carbohydrates, and lowest in summer and autumn. Seasonal variations in environmental conditions also affect the amino acid profile: lysine, for instance, disappeared in spring and summer whereas the concentration of aspartic acid (relative to protein content) doubled in winter (Galland-Irmouli et al., 1999).

Deposits of *Lithothamnion* and other calcareous red algae are mainly composed of calcium carbonate and contain about 30–35% of Ca.

5.3. Green seaweeds

Sea lettuce (*Ulva sp.*) has a good protein content (often >15% though lower values have been recorded) (Table 3) and low energy content (Arieli et al., 1993; Ventura and Castanon, 1998). Sea lettuce contain high insoluble dietary fibre (glucans) and soluble fibre (Lahaye and Jegou, 1993). *Ruppia maritima* and *Chaetomorpha linum* have a lower protein content (12–15%) (Ktita et al., 2010).

6. Inclusion in ruminant diets

The nutritive value of seaweeds for ruminants varies widely. It depends on the species, on the composition of the algae (protein, minerals, polysaccharides, phlorotannins) and also on the adaptation of the animal to this particular feed.

There are limited data on *in vivo* digestibility, *in sacco* degradability and energy values of seaweeds for ruminants. The *in vivo* energy digestibility of *U. lactuca* measured with young rams was 60% (Arieli et al., 1993). The *in vitro* organic matter digestibility of brown and red seaweeds, when measured with rumen fluid obtained from seaweed-fed sheep, was very high for brown algae *L. digitata*, *S. latissima* and *Alaria esculenta* species (94%, 97% and 81% respectively) and red algae *P. palmata* (81%), but was low for other brown seaweeds such as *A. nodosum*, *Fucus serratus* and *Fucus vesiculosus* (33%, 15% and 26% respectively) (Greenwood et al., 1983a). In a comparison of brown algae *M. pyrifera* and *Sargassum* species, the *in situ* DM degradability of the former was found to be low (50%) but higher than that of the latter (29%). Crude protein of these seaweeds was found to be rumen-undegradable *in situ*, but the *in vitro* trypsic digestibility of their proteins was high, which could make brown algae a good source of protein for ruminants despite their low protein content (Gojon-Baez et al., 1998). Effective degradability values for the green alga *U. lactuca* were also relatively low (54% and 41% for organic matter and protein degradability respectively) (Arieli et al., 1993). In any case, the high mineral content of seaweeds limits their gross energy content, and therefore their digestible, metabolizable and net energy values. Even a protein-rich (25%) alga like *U. lactuca* was found to have a digestible energy value of 9.1 MJ/kg DM (Arieli et al., 1993), similar to that of a good quality fodder.

Seaweeds are typically low in cellulose (about 4%) and rich in specific polysaccharides (alginate, laminarin and fucoidin) and in mannitol. Sheep that are usually fed with seaweeds, such as the Orkney sheep, have a rumen flora that does not include phycomycete fungi or cellulolytic bacteria but instead contain cilia species such as *Dasytricha ruminantium* and *Entodinium* species and lactate-utilizing bacteria such as *Streptococcus bovis*, *Selenomonas ruminantium* and *Butyrivibrio fibrisolvens* (Orpin et al., 1985; Greenwood et al., 1983b). As a consequence, the *in vitro* organic matter digestibility of seaweeds measured with rumen fluid obtained from grass-fed sheep (Orkney or another breed) was generally lower, particularly for *L. digitata* and *S. latissima*. For accurately assessing nutritive value of seaweeds using *in vitro* techniques it is vital to use rumen liquor from seaweed adapted animals. Seaweed feeding seems to change rumen microflora substantially, which may ensure a high degree of adaptation of rumen flora. Rumen ecology studies are warranted to obtain a better insight into the adaptation and adaptation mechanisms.

6.1. Brown seaweeds

6.1.1. A. nodosum

A. nodosum meal and its extracts have been used in ruminant diets for decades. The levels of supplementation mentioned in this article are on DM basis. For instance, *A. nodosum* is a common feed additive in dairy farms in the United States, notably in organically managed ones (Erickson et al., 2012). It is usually fed in low concentrations, typically less than 5%. *A. nodosum* has a low protein content and a high mineral content (Table 3), and therefore a low energy value. Also, *A. nodosum* meal is not very palatable and when fed to Holstein calves up to 60 g/d was found to depress DM intake. It was suggested that the presence of free glutamic acid, which enhances palatability in human food, may have an intake-depressing effect in calves (Erickson et al., 2012).

A. nodosum meal is therefore used in ruminants as an additive rather than to provide protein and energy. Early research found that it was a valuable source of minerals and could correct mineral-deficient diets for milk production, for instance by providing copper (Dunlop, 1953). More recently, *A. nodosum* meal and its extracts have been shown to enhance immunity and antioxidative status in cattle, sheep and goats (Allen et al., 2001a,b; Fike et al., 2001; Evans and Critchley, 2014). The meal increased the activity of superoxide dismutase, which is an antioxidant in both the forage and the grazing ruminant (Fike et al., 2001). In lambs and kids, *A. nodosum* meal enhanced immunity, improved the overall health of the animals and protected them against prolonged heat or transport-induced oxidative stress (Kannan et al., 2007a; Saker et al., 2004). This latter effect may be due to the presence of sodium chloride and potassium gluconate in *A. nodosum* (Archer et al., 2008). However, beneficial effects have not always been observed with transport-stressed animals and also did not last more than 3–4 days in cattle (Pompeu et al., 2011; Williams et al., 2009; Galipalli et al., 2004b; Carter et al., 2000). No alleviating effects on body weight losses or blood metabolite levels were shown in goats (Kannan et al., 2007b).

An *A. nodosum* extract containing large concentrations of phlorotannins (up to 500 μg/ml) linearly reduced *in vitro* fermentation both of mixed forage and of barley grain. Inhibition of *in vitro* ruminal fermentation was greater with cellulolytic bacteria than with amylolytic bacteria, which suggests that the influence of *A. nodosum* on animal performance depends on the diet (Wang et al., 2008). In steers, *A. nodosum* meal increased the slowly degraded protein fraction and protein degradability, and was more beneficial to forage digestibility when supplementing low-quality forage diets (Leupp et al., 2005). An increase in neutral detergent fibre digestibility by the meal has also been reported (Williams et al., 2009).

In feedlot cattle and lambs, *A. nodosum* meal supplemented at 2% for 2 weeks at the beginning of the feedlot period maximized carcass performance with no detrimental effect on performance and resulted in a prolonged shelf life of carcass (Anderson et al., 2006; Tavasoli et al., 2009). In meat goats, the addition of *A. nodosum* extract for 8 weeks before slaughter increased colour stability of loin/rib chops, even though there was no effect on lipid oxidation (Galipalli et al., 2004a).

In cattle and lambs, feeding *A. nodosum* meal at 2% during the 2 last weeks before slaughter reduced animal shedding of *Escherichia coli* O157:H7 (Bach et al., 2008; Braden et al., 2004, 2007), which possibly could be due to phlorotannins present in the meal (Wang et al., 2009, 2013b; Nagayama et al., 2002). Reduction in other pathogenic microorganism such as *Salmonella* sp., *Campylobacter* species and *Clostridia* in the gastrointestinal track of domestic animals has also been observed (Evans and Critchley, 2014). The addition of *A. nodosum* meal in animal diets could be a promising tool to increase food safety.

Feeding *A. nodosum* extract sprayed on the pasture or mixed in the diet decreased the body temperature in steers suffering from a fever caused by fescue toxicosis (due the infection of fescue with the fungus *Neotyphodium coenophialum*) (Saker et al., 2001; Spiers et al., 2004). Steers that had grazed the *A. nodosum* extract treated pastures had higher marbling scores and a better colour stability of the steaks (Allen et al., 2001a; Montgomery et al., 2001).

6.1.2. Laminaria and Saccharina

The Orkney sheep in the North Ronaldsay Islands feed almost exclusively on seaweeds for most of the year. Their preferred species are the brown algae *L. digitata*, *L. hyperborea* and *S. latissima* (formerly known as *Laminaria saccharina*). These species may account for up to 90% of the diet in summer, depending on availability. This diet could meet substantial amount of nutrient requirements as these species may contain up to 13% crude protein. The Orkney sheep also eat other brown algae such as *A. esculenta*, *A. nodosum* and *Fucus* species as well as red algae (*P. palmata*) and green algae (Hansen et al., 2003). Their activity pattern depends on the tidal cycle, because the sheep eat the algae at night when the tide is low (Paterson and Coleman, 1982). The sheep consume seaweeds in amounts high enough to sustain maintenance requirements, but they suffer from mineral overload (see Section 11) (Hansen et al., 2003).

6.1.3. M. pyrifera

M. pyrifera could be used up to 30% in the diet as a supplement for goats without affecting *in vivo* digestibility, *in situ* degradability and parameters of ruminal fermentation, such as pH and ammoniacal nitrogen (Mora-Castro et al., 2009). *In situ* DM digestibility was high (77–85%) (Gojon-Baez et al., 1998). Including *M. pyrifera* in the diet increased rumen pH, water intake and urine excretion (Mora-Castro et al., 2009).

6.1.4. Sargassum

Sargassum spp. could be introduced at up to 30% in the diets of growing sheep and goats without depressing intake, growth performance and diet digestibility (Casas-Valdez et al., 2006; Marín et al., 2003, 2009). Feeding *Sargassum* increased water consumption, probably due to their high concentration in minerals, notably Na and K, which could make *Sargassum* less suitable for feeding during dry periods. *Sargassum* meal could be used to limit the decrease in rumen pH resulting from acidogenic diets. It also tended to decrease the concentration of volatile fatty acids (Marín et al., 2009).

6.2. Red seaweeds

P. palmata has a potentially high nutritive value in ruminants (Greenwood et al., 1983a). In the 19th and early 20th century it was observed to be highly palatable to sheep, goats and cattle living in the shores of Northern and Western Europe (Brittany, Scotland, Scandinavia) (Sauvageau, 1920). However, neither *P. palmata* nor other non-calcareous red algae has received much attention as an animal feed in modern scientific literature. This alga has crude protein that can be as high as 26% DM in spring (Table 3) and hence could be a good source of protein when harvested at the right time. Further studies on true protein content, nature and contents of carbohydrate present and their availability would provide better information on its feeding value.

There have been several experiments about calcareous seaweed extracts. A *Lithothamnion calcareum* extract (containing 2.8% of Ca) fed at a ratio of 0.5 g/kg DM to steers receiving a diet with 70% concentrate had a buffering effect on rumen pH, but did not improve fibre digestion nor modify rumen fermentation (Montanez-Valdez et al., 2012).

In dairy cows, a by-product of agar production from *Phyllophara* added (100 g) to a diet deficient in copper, zinc and cobalt could increase milk yield by 4.4% and milk fat content by 0.24% units (Tolokonnikov et al., 1992).

6.3. Green seaweeds

Information on green algae for ruminants is limited. Sea lettuce (*U. lactuca*) could be fed to male lambs at up to 20% in a vetch hay/concentrate based diet without adversely affecting palatability of the diet. It had low protein degradability (40%) and also a moderate energy digestibility (60%). *Ulva* was considered to be comparable to a medium to low quality forage and suitable for use with feeds that have a high energy/low protein content such as cereal grains (Arieli et al., 1993).

In Tunisia, air-dried *C. linum* included at 20% in the diet of growing lambs (partially replacing barley) had a slightly depressing effect on growth and feed conversion ratio, possibly due to the higher ash content (Ktita et al., 2010). In the United Arab Emirates, an unspecified green seaweed harvested from fish ponds and dried was included in the diet of growing lambs at 1%. The seaweed meal slightly depressed the feed conversion ratio but showed a tendency to decrease meat fat and digestive tract fill (Al-Shorepy et al., 2001).

7. Inclusion in pig diets

In the 19th and early 20th centuries in Gotland (Sweden), pigs were fed with a mixture of boiled brown algae *F. vesiculosus* and cereal meal (Sauvageau, 1920). A similar use was reported in Loch Feochan (Scotland), where boiled or raw brown algae *Pelvetia* species were fed with oatmeal to fatten pigs (Chapman and Chapman, 1980). However, it has been shown that moderate to high amounts of brown seaweeds in the diet may be detrimental to pigs: for example *A. nodosum* meal fed to pigs at 10% in the diet did not affect blood parameters but weight loss was recorded after several weeks (Jones et al., 1979). Nowadays, seaweeds are fed as additives in low amounts (1–2%) for their potential benefits for pig health and meat quality.

7.1. Seaweeds as a iodine source

In regions where part of the population suffers from iodine deficiency, the use of seaweeds in pig feeding has been proposed to increase iodine concentration in pig meat, as the organic iodine found in seaweeds such as *Laminaria* or *Ascophyllum* is readily metabolized and stored in the pig muscle, unlike inorganic iodine (Banoch et al., 2010). Feeding pigs with a diet containing 2% of dried *A. nodosum* (the seaweed-based diet contained 10 mg/kg of iodine *vs* 1 mg/kg for the control diet) increased the concentration of iodine in animal tissues by 2.7–6.8, depending on the tissue. This feeding strategy for producing iodine-enriched meat was found to be an easily controllable contribution to human iodine supply, without risk for overdosing or the need for shift in eating pattern, but this contribution was considered insufficient to solve the actual iodine deficiency at country level in Belgium (Dierick et al., 2009).

7.2. Prebiotic and health effects

Seaweeds and seaweed extracts have been shown to have prebiotic effects and to enhance immune function in pigs, and have been assessed as potential antibiotic replacers in pigs. For instance, laminarin and fucoidan extracted from *Laminaria* species were found to improve piglet performance, with laminarin being the main source for gut health and performance improvements (Gahan et al., 2009; McDonnell et al., 2010). In contrast, there have been few trials with intact seaweeds. In Japan, seaweeds of unspecified species fed for four days, from 76 day- to 80 day-old pigs at 0.8% dietary inclusion increased IgA production in saliva and immune function (Katayama et al., 2011). In Belgium, *in vitro* investigations revealed a depressive effect of dried *A. nodosum* on piglet gut flora, especially on *E. coli*. Seaweed meal included at 1% in piglet diets reduced the *E. coli* load in the stomach and small intestine, while increasing the *Lactobacilli*/*E. coli* ratio in the small intestine, indicating a greater resistance to intestinal disorders (Dierick et al., 2009, 2010). However, in a later experiment by the same authors, the seaweed meal added at 0.25%, 0.5% or 1% to piglet diets of good digestibility failed to enhance performance of weaned piglets, gut health parameters, plasma oxidative status, and did not alter the microbial ecology in the foregut and in the caecum. This lack of effect could be due to the presence of phlorotannins in *Ascophyllum*, which would counteract the prebiotic effects of other compounds, or it could be due to a too low inclusion rate. With regards to the unchanged oxidative status, antioxidant vitamins in the diet may have masked the antioxidant effect of the seaweed (Michiels et al., 2012).

8. Inclusion in poultry

Seaweeds have been used in poultry to improve animal immune status, to decrease microbial load in digestive tract, and for their beneficial effect on quality of poultry meat and eggs (Abudabos et al., 2013; Wang et al., 2013a,b; Ali and Memon, 2008; Zahid et al., 2001). Inclusion rates are generally low (1–5%).

8.1. Broilers

8.1.1. Brown seaweeds

A. nodosum meal fed to broilers increased growth performance (Evans and Critchley, 2014). A comparison of raw, boiled or autoclaved *Sargassum* species included at up to 6% in broiler diets concluded that processed *Sargassum* did not have a better feed value than raw seaweed. Inclusion of *Sargassum* depressed growth but had no effect on dressing percentage and it enhanced polyunsaturated fatty acids and n-3 fatty acids, thus improving meat quality (El-Deek et al., 2011). Wakame (*U. pinnatifida*) included up to 4% in broiler diets were shown to alleviate the negative impact of induced acute phase response (the decrease or increase in the concentration of certain plasma proteins in response to inflammation), notably by reducing protein breakdown (Koh et al., 2005).

8.1.2. Red seaweeds

Calcified seaweeds are a valuable alternative source of calcium for broilers as availability of organic calcium is higher than that of inorganic calcium from mineral sources such as limestone. While high dietary concentrations of calcium from limestone decrease phosphorus digestibility, the lower concentrations made possible by calcified seaweeds result in better bone health and reduced leg weakness and lameness (Bradbury et al., 2012).

8.1.3. Green seaweeds

Green seaweed *Enteromorpha prolifera* fed to broilers at inclusion rates ranging from 2% to 4% provided best nutrient availability and high apparent metabolizable energy, which may be attributed to a high level of amylase in the duodenum. It had a positive effect on feed intake, feed conversion ratio and average daily gain while reducing abdominal and subcutaneous fat thickness, thus improving breast meat quality (Wang et al., 2013a; Sun et al., 2010). Inclusion of *U. lactuca* at 3% dietary level in broilers (12–33 day-old) had no effect on feed intake, body weight gain, feed conversion ratio and nutrient retention (Abudabos et al., 2013), while its inclusion at levels higher than 10% resulted in lower feed intake and reduced growth rate in 3 week-old broilers and cockerels (Ventura et al., 1994).

8.2. Laying hens

Brown seaweed *Sargassum* species from the Red Sea shore fed to laying hens during 20–30 weeks at 1–12% dietary level had no deleterious effect on body weight, egg weight, egg production, feed conversion ratio and egg quality (El-Deek and Al-Harthi, 2009). *Sargassum dentifolium* fed raw, boiled or autoclaved at levels of 3% or 6%, was beneficial to egg quality. It decreased yolk cholesterol, triglycerides and n-6 fatty acids and increased carotene and lutein plus zeaxanthin contents. Boiling improved high density lipoprotein, a desirable trait for human health (Al-Harthi and El-Deek, 2012).

Green seaweed *E. prolifera* included at 1–3% resulted in improved egg production and quality: it increased weight, shell thickness, and yolk colour and reduced cholesterol in yolk. It also resulted in a lower *E. coli* load in faeces, suggesting better animal health. Also it was found to decrease the feed conversion ratio (Wang et al., 2013b).

9. Inclusion in rabbit diets

9.1. Brown seaweeds

A. nodosum and *L. digitata* have been used as a part of the rabbit feed.

9.1.1. A. nodosum

A. nodosum fed to rabbits at 10% in the diet resulted in severe decreases in haemoglobin, serum iron and packed cell volume. It also led to body weight loss and death of most of the rabbits (Blunden and Jones, 1973). The use of *A. nodosum* as a feed ingredient for rabbits should therefore be avoided until further studies demonstrate its harmlessness and nutritional value. It must be noted that laminarin sulphate was found to be toxic to rabbits and dogs when it was tested as an anticoagulant in the 1950s (Kain et al., 1959).

9.1.2. L. digitata

In rabbits with experimental hyperlipoproteinemia, *L. digitata* fed at 1 g/d for 14 days lowered cholesterol and beta-lipoprotein (especially triglycerides), while it increased the level of high density lipoproteins HDL-C and HDL2-C without affecting HDL3-C and packed cell volume (Tang and Shen, 1989).

9.2. Red seaweeds

Calcified seaweeds such as *Lithothamnion* are used as a source of calcium for rabbits (Euler et al., 2008). In France, for instance, producers of organic rabbits have been reported to mix it with clay and salt and to place the resulting product in free access in a corner of the cage (Leroyer and Coulombel, 2009). *Lithothamnion* species introduced in rabbit diets up to 1% (replacing bentonite) had no significant effect on growth and slaughter performance or on diet digestibility, but reduced the length and width of intestinal villi. This could result from the increase in dietary calcium level from 0.9% to 1.5% (% diet as fed) (Euler et al., 2010).

9.3. Green seaweeds

In most studies on rabbits *Ulva* species have been investigated at low levels.

9.3.1. Ulva species

In a 120-day trial in Egypt, *U. lactuca* or *Ulva intestinalis* introduced at 1% as a feed additive in the diets of growing Baladi rabbits had a positive effect on growth performance and diet digestibility, the effect being more notable with *U. lactuca*. Haematological and biochemical parameters did not show any negative effects on rabbit health (El-Banna et al., 2005).

In Saudi Arabia, washed and sun-dried *U. lactuca* introduced at 1% or 2% in the diets of reproductive male and female rabbits during several weeks (from one week before insemination until kindling) reduced significantly the adult body weight in both sexes (−7 to −8%). It increased testosterone in males (+12%) and plasma oestrogens in females (+125%). Sperm concentration, percentage of live spermatozoa and ejaculate volume were reduced while sperm motility was improved. Due to the small number of artificially inseminated does (10 per treatment) no significant effect on reproduction parameters was observed at kindling (Okab et al., 2013).

In India, *U. fasciata* introduced up to 15% in growing rabbit diets, replacing the same proportion of the concentrate (distributed with 300 g/d of fresh alfalfa), did not affect growth rate, feed efficiency and carcass characteristics; but faecal consistency became looser as the inclusion rate of algae increased from 10% to 15%. A maximum inclusion rate of 5% was therefore recommended (Raju and Sreemannarayana, 1995; Sreemannarayana et al., 1995).

In a study from Tunisia, dried *Ulva* species was introduced up to 30% in rabbit diets with no alteration of growth performance and organic matter digestibility though it was associated with a reduction of carcass adiposity (Chermiti et al., 2009).

9.3.2. R. maritima

In southern Italy, dried *R. maritima* was proved usable for feeding growing rabbits (Finzi et al., 1979). In Tunisia, it could be introduced up to 30% in rabbit diets with no alteration of growth performance and organic matter digestibility though it was associated with a reduction of carcass adiposity (Chermiti et al., 2009).

More studies are required in rabbits to assess the full potential of seaweeds as a nutrient provider or as a source of bioactive compounds to be used as prebiotics.

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10. Environmental impact of seaweed harvesting

Seaweeds are home to many invertebrates that are prey for arthropods and marine birds and high collection rates of seaweeds have been reported to alter the equilibrium of coastal ecosystems. For instance, the harvest of wild kelp in Norway was found to be detrimental to fish abundance and to the foraging efficiency of birds (Lorentsen et al., 2010).

11. Potential constraints: heavy metals and mineral overload

Marine algae concentrate inorganic elements from seawater and may contain heavy metals and other mineral contaminants. For that reason, seaweeds for food and feed are subject to national and international regulations concerning their content in trace elements. In the European Union, calcareous marine algae must contain less than 10 mg/kg of arsenic, 15 mg/kg of lead and 1000 mg/kg of fluorine; seaweed meals and seaweed-based feed materials must contain less than 40 mg/kg of arsenic, and less than 2 mg/kg if requested by the competent authorities (all values relative to a feed with moisture content of 12%) (Commission Regulation N°574/2011 amending Annex I to Directive 2002/32/EC, 2011). The brown algae *S. fusiforme* (Harvey) Setchell (synonym *Hizikia fusiformis* (Harvey) Okamura) is known for its high concentration of arsenic and is singled out in the latter Commission Directive (Moreda-Piñeiro et al., 2012).

The Orkney sheep of the North Ronaldsay Islands feed almost exclusively on seaweeds and absorb large amounts of arsenic which are excreted *via* the kidneys or stored in tissue samples or wool, up to 100 times higher than the levels of unexposed sheep (Raab et al., 2002; Feldmann et al., 2000; Martin et al., 2005). The high mineral content of algae has deleterious effects on the health of Orkney sheep: they suffer from severe dental disease precipitated by heavy deposits of tartar and from extensive mineralization of the kidney medulla (Britt and Baker, 1990).

Seaweeds, particularly brown algae, contain high amounts of iodine and may cause iodine poisoning when fed during prolonged periods. In the European Union, the maximum iodine concentrations proposed in complete feeds are 2 mg/kg (dairy ruminants), 3 mg/kg (laying hens) and 3 mg/kg (horses) (EFSA, 2013). The decomposition of seaweeds containing these toxic constituents on the beaches could be source of intoxication of grazing animals (ANSES 2010-SA-0175, ANSES 2010-SA-0225).

12. Conclusions and way forward

Some seaweeds have the potential to contribute to the protein and energy requirements of livestock, while others contain a number of bioactive compounds, which could be used as prebiotic for enhancing production and health status of both monogastric and ruminant livestock.

The green alga sea lettuce (*U. lactuca*) has good protein content (*ca* 19%) and its digestible energy, while not very high, is similar to a good quality fodder (*ca* 9 MJ/kg). The rumen degradability of proteins in this seaweed is low (41%) and if the post-rumen degradability is high (no information available so far), it could be a good protein resource for high producing ruminant livestock. In a similar vein, rumen undegradable protein in brown algae, *M. pyrifera* and *Sargassum* species is also low, but *in vitro* trypsic digestibility of their proteins is high. *M. pyrifera* and *Sargassum* species have been added at levels of up to 30% in diets of goats and sheep without any adverse effects. Red seaweed *P. palmata* also has high crude protein content (*ca* 19%); however little is known about degradability of their proteins, in the rumen or post-rumen. Further studies are required to assess rumen undegradable protein and post-rumen degradable protein levels in these seaweeds and especially in *U. lactuca* and *P. palmata*; and to explore their potential to use as a source of post-ruminally available proteins. Information on the proportion of true protein to non-protein nitrogen is also required. Information available so far on amino acid composition shows that seaweeds are deficient in essential amino acids except sulphur containing amino acids.

L. digitata also has good level of protein (8–15%) and high *in vitro* organic matter digestibility (94%), suggesting it to be a good feed resource. Similarly *in vitro* organic matter digestibility of *S. latissima* and *A. esculenta* is high (97% and 81% respectively). Most seaweeds are rich in minerals which may give high *in vitro* dry matter degradability and low energy provision to animals. Also richness in minerals could make some seaweeds an inappropriate feed in water-deprived and drought situations due to high demand of drinking water required to excrete minerals from the body. On the other hand, the mineral richness of seaweeds and their presence in organic form could be exploited to provide organic minerals (availability of minerals from organic form is higher than from inorganic form) by strategically mixing various seaweeds that complement minerals, to give a cocktail having a required level of the minerals; realizing that one seaweed will not be in a position to meet requirement of all the mineral. Some calcified seaweeds (*e.g. Lithothamnion*) could be a good source of calcium for lactating animals, growing animals and laying hens. It may also be used in broilers to improve bone health and reduce leg weakness and lameness.

Seaweeds tend to accumulate heavy metals (arsenic), iodine and other minerals, and feeding such seaweeds could deteriorate animal and human health. Regular monitoring of minerals in seaweeds would prevent toxic and other undesirable situations.

Seaweeds contain a number of complex carbohydrates and polysaccharides. Brown algae contain alginates, sulphated fucose-containing polymers and laminarin; red algae contain agars, carrageenans, xylans, sulphated galactans and porphyrans; and green algae contain xylans and sulphated galactans (Evans and Critchley, 2014). Step-wise increase in the levels of seaweeds in the diet may enable rumen microbes to adapt and thus enhance energy availability from these complex carbohydrates. Advances made lately in molecular tools allow study of rumen and gut ecology without culturing of microbes. Using these tools the study of rumen and gut ecology in response to seaweeds would provide a better insight into their interactions with rumen and gut microbes, mechanism of adaptation of rumen microbes to seaweeds, resulting in better utilization of seaweeds as a feed resource or as a prebiotic for both ruminants and monogastrics. Also use of commercially available carbohydrases, a mix of proteases and carbohydrases or use of a biophysical process could enhance utilization of seaweeds containing complex carbohydrates. These carbohydrates as well as simple carbohydrates such as ascophyllan and other bioactive compounds such as phlorotannins present in seaweeds act as prebiotics for both ruminant and monogastric animals when seaweeds are given at low doses of up to 5% in diet. From the discussion in the aforementioned sections it can be deduced that in general seaweeds should be included in the diets of poultry and pigs only at low levels, usually up to 5–6% in growing animals and not above 10% in any case.

Increase in productivity (increase in growth and milk production) and quality (enhanced polyunsaturated fatty acids and n-3 fatty acids in meat) and safety (decrease in shedding of *E. coli* O157:H7, reduction in pathogenic microorganisms in gastrointestinal tracks) of animal products; and increase in immunity, antioxidative status and health have been reported. Also phlorotannins could act as a substitute for antibiotic growth promoters. However, further in-depth studies on these aspects, including impact on reproductive efficiency of animals are warranted.

In vitro treatment of seaweeds with enzymes cocktails available commercially (mix of proteases and carbohydrases) may also be exploited to generate novel carbohydrates and polysaccharides for use as prebiotics. In the future, equally important would be to well characterize seaweeds for carbohydrate and polysaccharide types and contents, so as to have a well-defined prebiotic with reproducible effects. The diet is also important in eliciting the desired effects of prebiotics. There is also a need to study interactions between diets and well characterized seaweeds or defined products isolated from seaweeds for possible use as prebiotics.

Other future areas of work are to develop easy, cost effective and environmentally friendly large scale production, harvesting and drying methods and tools for seaweeds that have potential for use in animal diets.

Conflict of interest

None declared.

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