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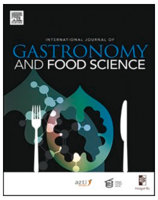

Review Article

Umami taste in edible seaweeds: The current comprehension and perception

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ABSTRACT

The fifth basic taste - umami, described as the essence of deliciousness, was discovered more than a century ago in Japan, after extraction of free glutamate from dashi, the Japanese broth prepared with brown seaweed *Saccharina japonica* (konbu). Although umami was accepted as a basic taste in the Eastern world a long time ago, umami gained recognition in the Western world very slowly. However, as the consumer's longing for delicious food is constantly growing, umami taste can be an important choice criterion. Moreover, in recent years, there has been an increasing demand for vegetarian and vegan products and edible seaweeds are a resource that has been used in the development of new food products. Consumption of edible seaweeds is becoming popular worldwide, not only due to their abundance and unique flavors but also because of their nutritional benefits and umami taste.

In this review, the basic concepts of umami in seaweeds are described. The traditional consumption of seaweeds in the Eastern world, but also the more innovative approach in Western countries, are referred. The quantification of compounds responsible for the umami taste in aqueous extracts (broths) based on edible seaweeds was reviewed. Also, the influence of seaweed conservation techniques (drying techniques applied) and extraction conditions on umami potentials have been discussed, as well as the latest studies on metabolic pathways, including the biochemical reactions between glutamate and umami receptors.

Introduction

In recent years, there has been an increased interest in seaweed (macroalgae) consumption worldwide, and accessible data show that the world seaweed market has grown by around 20% in the last 20 years (FAOUN, IFAD and WFP, 2020). Moreover, considering the current nutritional trends, food security, and sustainability issues, alternative sources of proteins will soon be needed to meet increased consumer demands and the expected global protein requirements (FAOUN, IFAD and WFP, 2020; Seaweed Manifesto, 2020; FAOUN, IFAD and WFP, 2020). Proteins of animal origin are rich in essential amino acids (EAA), whereas alternative plant-based proteins commonly lack some EAA, such as methionine, phenylalanine, tryptophan, etc. (Young and Pellett, 1994). Seaweeds are a source of lysine, an EAA often present in limited quantities in terrestrial plant-protein sources, such as corn, maize, soy, and wheat (Cherry et al., 2019). On the other hand, due to the high levels of saturated fatty acids and cholesterol in animal-protein sources, typically correlated with cardiovascular diseases and diabetes, plant-based proteins along with reduced consumption of fat, sugar, and salt, are highly recommended for a healthy and balanced diet (FAO, 1991; Scott, 2017). Compared to crops (e.g., soybean, legumes, wheat), the seaweeds are a better source of proteins, in terms of productivity and nutritional value (Bleakley and Hayes, 2017; Wells et al., 2017). However, *in vitro* studies showed that protein bioavailability was higher in red seaweeds than in green species, whereas brown species showed the lowest protein bioavailability due to their higher content of polysaccharides and dietary fibers (Fleurence, 1999; Wong and Cheung, 2001a; Rioux et al., 2017).

Based on updated documents from the Food and Agriculture Organization (FAO) of the United Nations, the Republic of Korea is currently the largest consumer of edible seaweeds (22.4 kg/capita/year) followed by China and Japan (FAO, 2013). The consumption of seaweeds is becoming very popular in gastronomy (e.g., sushi food, broths, ice-creams, bread, etc.), resulting in high commercialization of diverse phycogastronomy (gastronomy based on seaweeds) products. Seaweeds are considered as a sustainable source of macronutrients (dietary fibers),

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minerals, vitamins, and trace elements, such as iodine (MacArtain et al., 2007; Holdt and Kraan, 2011; Roohinejad et al., 2017). Besides this valuable nutritional composition, another prominent feature of edible seaweeds is their umami taste which, in addition to deliciousness, can contribute to reduce salt consumption, which is of great importance for a healthy diet (Fuke and Shimizu, 1993; Mouritsen et al., 2019a). Umami from konbu is used to flavor some dishes in the Japanese cuisine, thus producing healthier and tastier meals with reduced salt, sugar and fat contents (Fujii, 2005; Antony et al., 2014; Mouritsen and Styrbæk, 2014; Japanese Culinary Academy, 2016). Similarly, it was shown that the replacement of salt with soy sauce (rich in umami) can reduce up to 50% of salt consumption without decreasing costumer acceptance (Kremer et al., 2009; Goh et al., 2011). It is known that the ionic form of monovalent glutamic acid, i.e., glutamate is the main component of the umami taste (Ikeda, 2002). In addition, other amino acid salts, such as aspartate, have recently been discovered to contribute to the umami taste in seaweeds (Choudhury and Sarkar, 2017). In addition to the ionic form of amino acids, primarily glutamate and aspartate, some other compounds, such as organic acids (e.g., lactic, succinic, and propionic acids), and many short peptides can also elicit umami taste (Chaudhari et al., 2009).

Besides seaweeds, umami compounds can also be found in various plant materials. A key feature of umami in some vegetables is the presence of 5′-nucleotides, such as monophosphate esters of guanosine (GMP) and inosine (IMP), which have also been described as umami enhancers with synergistic effect on umami taste (Kuninka, 1960; Yamaguchi, 1998). It was shown that their mixture can produce a strong umami taste, but each one of them individually does not elicit any taste (Kuninka, 1960; Kurihara and Kashiwayanagi, 1998). In 2005, it was shown that a stronger umami taste, up to eight times, can be obtained if all components (NEAA + 5′-nucleotides) are included together, while when used separately their taste is very weak (Marcus, 2005). Nevertheless, IMP is predominately found in animal products (e.g., chicken, pork beef, tuna), and GMP is mainly found in mushrooms (Ninomiya, 1998; Yamagauchi et al., 2000; Hajeb and Jinap, 2015; Kurihara, 2009, 2015; Greisinger et al., 2016).

In the last two decades, based on the global research database (Science Direct, Scopus, and Web of Science), the references on free umami in edible seaweeds have not exceed the number of 40. However, comparing with the available data on umami in some other protein-rich sources, such as mushrooms, the total number of publications retrieved in the same period is four-folded (Sun et al., 2020). Therefore, the modern research has focused on other sources of umami rather than seaweeds, indicating that the fifth basic taste in edible seaweeds remained relatively poorly understood. The available literature shows that the content of umami free amino acid(s) in edible seaweeds is less studied in the Western world (Mouritsen et al., 2012; Hamid et al., 2018; Stévant et al., 2018; Poojary et al., 2019; Milinovic et al., 2020).

Through a compilation of free glutamate contents analyzed in water extracts of seaweeds worldwide, this review summarizes the umami potential of seaweed-based broths. The impact of seaweeds conservation (drying techniques), storage and extraction conditions on the free glutamate content and their contribution to umami, were overviewed. Thus, this work outlines a strong need for further research studies on edible seaweed species, in which better promotion of phycogastronomy could be based, especially in Western societies.

Umami taste in edible seaweeds

Discovery of the umami taste and its stimuli in edible seaweeds

Edible seaweeds have been widely consumed for several centuries, not only because of their availability but also because of their nutritional benefits. This tradition was maintained in Eastern culture, but the same has not occurred in the Western world (Mouritsen et al., 2012; Mouritsen and Styrbæk, 2014; Greisinger et al., 2016; Palmieri et al., 2020; Pérez-Lloréns et al., 2020).

At the beginning of the previous century, in 1908, the Japanese scientist at the Imperial Tokyo University, Kikunae Ikeda, discovered the main compound responsible for the umami taste in dashi (traditional Japanese broth based on seaweeds) prepared with brown seaweed species *Saccharina japonica* (konbu), commonly used in Japanese cuisine, by isolating glutamate (Yamaguchi and Ninomiya, 1998; Ikeda, 2002; Ogiwara and Ninomiya, 2002; Nakamura, 2011; Osawa, 2012; Hajeb and Jinap, 2015). Ikeda then concluded that the glutamate was the predominant stimuli of a new taste, that he called umami. The Japanese word ‘*umai*’ means brothy, meaty, or savory, while ‘*umami*’ describes a cognitive category of taste, with definitions that include deliciousness, flavor, relish, gusto and zest (Halpern, 2002; Ikeda, 2002). The term ‘umami’, designating the fifth taste (in addition to salty, sweet, sour, and bitter), was scientifically introduced at the first International Symposium that took place in Hawaii, in 1985 (Ninomiya, 2002). It was then categorized as a basic taste because it is different from any other basic taste or any combination of them and is common in food (Hartley et al., 2019). However, a biostatistical study carried out in selected groups of Japanese subjects, showed that among Japanese population, only workers and/or panel tasters involved in glutamate manufacture, could add a fifth taste label “ajinomoto”, referring to the taste of umami (O’Mahony and Ishii, 1986). On the other hand, the Americans could not assign a label to describe umami as a separate taste (O’Mahony and Ishii, 1986). In a recent comprehensive survey on umami familiarity in three European countries, Finland, Germany, and Italy, the 15% of the Finnish participants used the correct word ‘umami’, whereas for the other two groups only 2% of the participants did it (Cecchini et al., 2019). Moreover, in the same study, Finnish participants showed better discrimination between the MSG (umami) and sodium chloride (cooking salt) solutions. Thus, although more than one century has passed, the fifth basic taste concept has been slowly accepted in the global population of the Western world, not just because there is no common umami-forward stock in the Western cuisine that provides a sensation of umami (such as dashi), but also because of the differences in the taste sensation of monosodium glutamate (Lindemann et al., 2002; Mouritsen et al., 2012).

Seaweeds characteristics and classification - overview

Seaweeds are a large group of plants that occupy coastal areas and can have different shapes, sizes, and colors (Hasan and Chakrabarti, 2009; El Gamal, 2012). Based on pigmentation, seaweeds are divided into three main phyla: green (*Chlorophyta*), red (*Rhodophyta*), and brown (*Phaeophyceae*) (MacArtain et al., 2007; Kadam and Tiwari, 2013; Makkar et al., 2016). This difference in the pigments that seaweeds contain is correlated with their location in diverse aquatic environments and with their abundance (Pereira, 2009). Currently, there are more than 10,000 identified species, among which several hundred are edible (Pereira, 2011).

Green seaweeds are a diverse group of approximately 8000 species, containing pigments chlorophyll *a* and *b*, and beta-carotene and xanthophylls (Kadam et al., 2013). The most consumed species belong to the genus *Ulva* spp. (sea lettuce).

Red seaweeds comprise approximately 6000 species and phycobilins are responsible for their red color (Kadam et al., 2013). *Chondrus crispus* (Irish moss), *Porphyra* spp. (nori), and *Palmaria palmata* (dulse) are among the species most used by the food industry worldwide (Mouritsen et al., 2013a, 2013b). Some species of *Porphyra spp.* (nori) are relatively rich in proteins (up to 45% of the dry weight, dw) but these levels depend on the species and harvesting conditions (Fleurence, 1999). Being very rich in proteins, *Palmaria palmata* can contain as much as 35% of proteins, per dry weight of seaweed, with lower levels of glutamic and aspartic acid (equal to 14% of the total amino acids) (Fleurence, 1999).

Brown seaweeds are characterized by the presence of the fucoxanthin pigment, which is responsible for their granite-brown color (Kadam et al., 2013). They are the largest seaweeds with a length of up to 45 m in some species (Makkar et al., 2016). The number of species belonging to this group is around 2,000, and among them, the most consumed are the following: *Fucus evanescens* (bladderwrack), *Saccharina japonica* (kelp), *Saccharina latissima* (sugar konbu), *Laminaria digitata* (oarweed), and *Undaria pinnatifida* (wakame) (Fitzgerald et al., 2011).

For most species glutamic and aspartic acid constitute a large part of the amino-acid sequence of the proteins. Brown seaweeds have the highest levels of proteins, and glutamic and aspartic acid, whereas red seaweeds have lower levels of these amino acids (Fleurence, 1999; MacArtain et al., 2007). EAA such as histidine, leucine, isoleucine, and valine are present in many seaweeds, for ex., in *Palmaria palmata* and *Ulva* spp., while cysteine generally has a very low content (MacArtain et al., 2007).

Consumption of seaweeds worldwide: Eastern vs. Western world

Seaweeds have been consumed for thousands of years, notably in the Eastern world, particularly in some Asian countries, such as China, Japan, Korea, and Polynesia, where gastronomy is traditionally based on seaweeds since ancient times (Chapman and Chapman, 1980; Otsuka, 1998; Holdt and Kraan, 2011; Mouritsen et al., 2018; Badmus et al., 2019). The annual consumption of seaweeds in Japan and Korea is estimated to exceed 93% of the total amount of seaweeds harvested in these countries (McHugh, 2003; Mouritsen et al., 2019b). According to the Japanese National Health and Nutrition survey, in Japan, seaweeds consumption in 2014 was estimated to be 9.6 g of seaweed/day per adult (MHLW, 2014). This is justified by tradition and long roots of nutrition based on minimally processed seaweeds. In Japan, 21 species of seaweeds are included in the diet, in Polynesian islands and Hawaii more than 25 species are used as food and medicine, whereas in Korea about 40 types of seaweeds are used in gastronomy (Arasaki and Arasaki, 1983). *Saccharina japonica* (kelp) has been used for centuries for food purposes in China, Japan, and Korea (Holdt and Kraan, 2011). Dried konbu was typically consumed in soups, salads, and tea or it was used to make secondary products with various seasonings (Lobban and Harrison, 1994). In Korea, *Undaria pinnatifida* (wakame) is used to make miyeok-guk, a soup traditionally consumed after delivery (Pérez-Lloréns et al., 2020). In the Indo-Pacific region diverse *Gracilaria* species are consumed as sea vegetables (Norziah and Ching, 2000; Gaillande et al., 2007; Mouritsen et al., 2018).

On the other hand, the situation in the Western society is quite distinct, with no relevance of conserved traditional uses of seaweeds in the diet. More precisely, less than 1% of totally harvested seaweeds at national levels, are consumed in the USA and Europe (McHugh, 2003; Mouritsen et al., 2019b). In the USA and Canada, seaweed consumption is mostly oriented towards imported Asian dishes, such as sushi (Rioux et al., 2017). Only in a few places, i.e., in Chile, Ireland, and Peru, seaweeds have been conserved as a food resource (Mouritsen et al., 2018). As a part of local traditional cuisine, laverbread, a food product based on *Porphyra* spp. is often consumed in Wales (Wells et al., 2016; Godlewska et al., 2017; Mouritsen et al., 2018). In Portuguese island Azores, the known traditional recipes are pies, made with various species of *Ulva* spp. and *Porphyra* spp. (Matos, 2013; Mouritsen et al., 2018; Alga4Food, 2020).

Additional consumption of seaweeds is achieved through some polysaccharides i.e., phycocolloids (e.g., agar, carrageenan, and alginates synthetized in cell walls of red and brown seaweeds, respectively), that are extensively used as thickening, emulsifying, stabilizing, and gelling agents by the food industry (Holdt and Kraan, 2011; Roohinejad et al., 2017; Wells et al., 2017). In Japanese cuisine, yokan is a desert traditionally made with agar (Rioux et al., 2017; Mouritsen et al., 2018). In Ireland, *Chondrus crispus* (Irish moss) is traditionally used in many recipes, of which the most popular is Irish moss pudding (Rioux et al., 2017). Mannitol is a type of sugar alcohol which is often found in the *Saccharina* family, particularly in *Saccharina latissima* (sugar kelp), and it has potential application as a sweetener (Mouritsen et al., 2012, 2019b; Rioux et al., 2017).

The most recent promotion of phycogastronomy began in some Nordic countries, Spain, and Australia, by introducing several edible seaweeds in dishes (Mouritsen et al., 2012, 2019b). To extend the use of seaweeds in gastronomy, the collaboration between scientists and chefs has been encouraged and intensified. There have been attempts to promote the gastronomic potential of local edible seaweeds in the New Nordic Cuisine (Redzepi, 2006, 2010; Mouritsen, 2012a, 2012b; Mouritsen et al., 2013a, 2013b, 2018, 2019b; Mouritsen and Styrbæk, 2014). For example, a few recipes, of bread, cheese, and ice cream, mixed with *Palmaria palmata* (dulse), as umami flavoring, have been suggested (Mouritsen et al., 2012).

The extension of Portugal's continental shelf (approximately 97% of it is the Atlantic Ocean) has motivated researchers to study the seaweeds available in its waters as well as to explore its potential as a food resource. Several works have already been published, with the list of edible seaweed species from the Portuguese coast and their nutritive values (Pereira, 2011; Soares et al., 2017; Vieira et al., 2018). The project 'Alga4Food' at the NOVA University Lisbon, in Portugal, is a recent multidisciplinary project, focused on the promotion of the use of seaweeds in gastronomy (Alga4Food, 2020). The 'Alga4Food' project envisages exploring the benefits of edible seaweeds from the Portuguese coast, through the development of innovative conservation and utilization techniques. The project includes strategies for introducing seaweeds into the Portuguese diet, by including them in some of the traditional recipes (Fig. 1).

An interesting recent study, involving Italian consumers, reported an increased interest in seaweeds consumption. For instance, from a sample of 257 consumers, about 76% were willing to eat seaweeds, and this was explained by the consumer's familiarity with traditional dishes from Asian gastronomies (Palmieri and Forleo, 2020). From a functional and emotional benefit standpoint, consumers in the USA reported feeling significantly higher levels of positive emotions, such as happiness, excitement, indulgence, etc., after eating foods rich in umami, compared to the controls (Miyaki et al., 2016). All these facts can serve as an excellent motive for increased seaweed consumption in Western countries.

Fig. 1. Traditional 'Gazpacho' with red seaweed *Fucus vesiculosus.* (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

Umami chemistry

Free glutamate in edible seaweeds

The high consumption of seaweeds in some Asian countries is correlated with their significant protein content, and particularly with a high content of free glutamate which contributes to the delicious umami taste in some species (MacArtain et al., 2007). Conversely, other protein-rich foods, including meat, do not contain high concentrations of free glutamate and are quite tasteless, unless submitted to several cooking processes (e.g., fermentation, heat cooking or curing treatments), that induce proteolysis and thus release amino acids and peptides, which stimulate umami taste responses (Yoshida, 1998; Hartley et al., 2019).

Most of the research studies focused on the total content of amino acids obtained upon acid hydrolysis of seaweeds (Norziah and Ching, 2000; Wong and Cheung, 2001b; Sánchez-Machado et al., 2003; Peinado et al., 2014; Astorga-España et al., 2016; Ishakani et al., 2017; Vieira et al., 2018; Badmus et al., 2019; Bruno et al., 2019), while only in a few studies umami free amino acids (glutamate and aspartate) were quantified.

The umami potential is reviewed in studies of aqueous extracts (broth) of seaweeds, with the focus on their use in gastronomy. Table 1 shows systematic data on free glutamate, min-max values expressed in mg (100 g)$^{-1}$ dw, obtained in the comparative analysis of edible species of green, red, and brown seaweeds, from around the world. Since the relative umami concentration for aspartate (0.077) is much lower than for glutamate (1), its contribution to the equivalent umami concentration is negligible. Moreover, its concentrations in most species are rather low and hence, they were not discussed in most of the available works (Yamaguchi et al., 1971; Li et al., 2002; Mau, 2005; Chandrashekar et al., 2006; Mouritsen et al., 2012).

As can be seen, the three main phyla of seaweeds, showed a wide range of umami potential. Variations in umami potential in different seaweed species can be explained by several factors, including the difference in harvest conditions (e.g., season, an ecology of location), characteristics of the species (e.g., maturity, quality), and/or maturation effect i.e., aging of the dried species (Stévant et al., 2018, Badmus et al., 2019; Cherry et al., 2019). Additional factors can be associated with the physico-chemical parameters of water (salinity, temperature, pH, etc.), depth of the collected seaweed species, and post-harvest conditions (Myhrvold et al., 2011).

The lowest glutamate concentrations were found, among others, in green seaweeds, *Codium tomentosum* (Codium) and *Ulva rigida* (sea lettuce) from the Portuguese coast, whereas some red species had higher levels of free glutamate, up to 1378 mg (100 g)$^{-1}$ dw, such as *Pyropia* sp. *(nori)* from Japan (Ninomiya, 1998). As can be observed, red phylum of seaweeds (Rhodophyta) showed a broad range of glutamate content, differing by three orders of magnitude. *Gracilaria verrucosa* (graceful red weed), contained very low levels of free glutamate, i.e., 5 mg (100 g)$^{-1}$ dw of seaweed, whereas other species contained significant levels of several hundred, including *Chondrus crispus*, *Gracilaria gracilis,* and *Osmundea pinnatifida* (Ninomiya, 1998; Mouritsen et al., 2012; Milinovic et al., 2020). Therefore, they are comparable with some vegetables, which contain high levels of umami. For example, umami in potatoes and tomatoes was found in a range of 180–246 mg (100 g)$^{-1}$ (Ninomiya, 1998). The results presented in Table 1, show that some red seaweeds, in particular *Chondrus crispus*, *Gracilaria gracilis,* and *Osmundea pinnatifida* may constitute an adequate umami-rich nutrient with higher umami potential compared to some vegetables. The species of *Palmaria palmata* (dulse) from Denmark, had free glutamate in concentrations from 40 to 205 mg in 100 g (dw) of seaweed (Mouritsen et al., 2012; Poojary et al., 2019).

The brown species of *Saccharina japonica* (Ma-konbu kelp) and *Laminaria digitata* (konbu) showed the highest umami potentials, with maximum concentrations equal to 1608 and 2240 mg (100 g)$^{-1}$ dw,

Table 1
Free glutamate (mg (100 g)$^{-1}$ dw) in seaweed species worldwide.

Seaweed species	Common name[a]	Location	Free glutamate mg (100 g)$^{-1}$ dw	Reference
Chlorophyta (green)				
Codium tomentosum	Codium, Chorão-do-mar	Portugal	18–55	Milinovic et al. (2020)
Ulva rigida	Sea lettuce	Portugal	13–51	Milinovic et al. (2020)
Rhodophyta (red)				
Chondracanthus teedei var. *lusitanicus*	–	Portugal	58–283	Milinovic et al. (2020)
Chondrus crispus	Irish moss	Portugal	133–627	Milinovic et al. (2020)
Gracilaria gracilis	Cabelo-de-velha	Portugal	398–499	Milinovic et al. (2020)
Gracilariopsis longissima	Graceful red weed	Denmark	5	Mouritsen et al. (2012)
Grateloupia turuturu	Ratanho	Portugal	44–186	Milinovic et al. (2020)
Nemalion helminthoides	Sea noodles	Portugal	69–249	Milinovic et al. (2020)
Osmundea pinnatifida	Botelho-preto	Portugal	261–314	Milinovic et al. (2020)
Palmaria palmata	Dulse	Denmark	40–205[b]	Mouritsen et al. (2012); Poojary et al. (2019)
		Iceland	10	Mouritsen et al. (2012)
Pyropia sp.	Nori (dried laver)	Japan	1378	Ninomiya (1998)
Phaeophyceae (brown)				
Bifurcaria bifurcata	Frosque	Portugal	14–74	Milinovic et al. (2020)
Fucus evanescens	Bladderwrack	Denmark	90–276[b,c]	Mouritsen et al. (2019a); Poojary et al. (2019)
Fucus vesiculosus	Rockweed, Fava-do-mar	Denmark Portugal	70[c] 62–164	Mouritsen et al. (2019a) Milinovic et al. (2020)
Saccharina japonica (formerly *Laminaria japonica)*	Ma-konbu kelp	Japan	550–1608[c]	Ninomiya (1998); Mouritsen et al. (2019a)
Saccharina latissima (formerly *Laminaria saccharina)*	Sugar kelp	Denmark	3–55[c]	Mouritsen et al. (2012); Mouritsen et al. (2019a)
		Germany	97[b]	Poojary et al. (2019)
Laminaria digitata	Konbu or Kombu	Japan	70–2240	Ninomiya (2002); Mouritsen et al. (2012)
		Norway Iceland Denmark	151 155[c] 28[c]	Stévant et al. (2018) Mouritsen et al. (2019a) Mouritsen et al. (2019a)
Saccorhiza polyschides	Furbelows	Portugal	32–100	Milinovic et al. (2020)
Undaria pinnatifida	Wakame	Japan France	9–195[c] 0.75[c]	Ninomiya (1998); Mouritsen et al. (2019a) Mouritsen et al. (2019a)
		Portugal	24–40	Milinovic et al. (2020)

[a] Chapman and Chapman (1980); Pereira (2009); Mouritsen et al. (2012); Guiry and Guiry (2020).

[b] The sum of amount of free glutamate and aspartate.

[c] The concentration of glutamate in mg (100 g^{-1}) dw), is calculated based on the information given for dashi preparation (Mouritsen et al., 2019a).

respectively (Ninomiya, 1998, 2002). In species of brown *Saccharina japonica* (from Japan) very broad range, from 550 up to 1608 mg per 100 g dw of seaweed (Ninomiya, 1998; Mouritsen et al., 2019a) can be attributed to the quality of harvested species. The studies by Mouritsen et al. (2019a), were carried out with different commercial supplies of dried *Saccharina japonica* (Hokkaido, Japan) of distinct qualities: a first-quality raushu-konbu showed higher values in free glutamate (1150–1350 mg (100 g^{-1}) dw) in comparison to a second-quality hidaka-konbu (215–900 mg (100 g^{-1}) dw). This wide range of results can be explained by several factors, such as the maturity of the species, harvesting conditions (season, ocean temperature, pH, or salinity), post-harvest storage, seaweed treatments, etc. (Mouritsen et al., 2012, 2019a; Wells et al., 2017). Despite the difference in their anatomy, all seaweeds are similar in their use of amino acids to counteract the salinity of the seawater environment (Myhrvold et al., 2011). The variation in salinity, can partly explain the different flavors of seaweeds from different waters.

Besides konbu and kelp, being the species with the highest content of free glutamate, some other brown species can also provide noticeable umami taste, such as *Bifurcaria bifurcata*, two species of genum *Fucus*, *Saccorhiza polyschides*, and *Undaria pinnatifida* (wakame). Although it shows a relatively low umami potential, *Undaria pinnatifida* has been widely used in gastronomy (e.g., noodles, soups, and pickles) because it is an excellent source of nutrients (Taboada et al., 2013; Wells et al., 2017).

It can be concluded that the results on the free glutamate content are scarce and among hundreds of known edible species, only a few green, red, and brown seaweeds from several countries worldwide have been studied. The few studies on the umami potential in seaweeds can be associated with their low use in gastronomy, especially in Western countries. Clearly, the results show that among the studied seaweeds, besides brown (konbu and kelp), some red species such as *Chondrus crispus*, *Gracilaria gracilis,* and *Osmundea pinnatifida*, could be also considered, as worthy candidates for umami flavoring. These and some other edible species should be more studied, with the focus on their use in gastronomy as seasoning agents in e.g., broths, marinating media, dressings, and sauces.

Influence of seaweeds conservation and extraction conditions on umami potential

Variations in umami potential in the same species can be explained by conservation (e.g., drying techniques), and/or storage conditions (Stévant et al., 2018, Badmus et al., 2019; Cherry et al., 2019). In a work recently published on free umami compounds in edible seaweeds from the Portuguese coast, the same species showed a wide range of concentrations of free glutamate (e.g., *Chondracanthus teedei var. lusitanicus, Chondrus crispus, Grateloupia turuturu*), being the differences associated to the drying techniques applied to the seaweed samples, i.e., oven-dried vs. lyophilized samples (Milinovic et al., 2020). The results indicated that lyophilization constitutes a superior procedure to increase the umami potential in most of the selected seaweeds.

Besides conservation techniques of seaweeds, the origin of the seaweeds and the extraction procedures can be important for the quantification of the umami compounds content. As an example, in the analysis of red seaweed *Saccharina latissima* (sugar kelp), Poojary et al. (2019) used a dried commercial product (from Germany) and extraction at 50 °C during 30 min, while Mouritsen et al. (2012), analyzed sun-dried seaweed species (farmed in the open coastal waters in Denmark) after water-extraction at 60 °C during 45 min. The origin and the slight differences in the extraction process can explain the broad range in results obtained for glutamate in *Saccharina latissima* (sugar kelp), however it is impossible to quantify the influence of each of these factors.

Considering the extraction conditions, it has been shown that the use of well-controlled parameters improves the extraction efficiency for free glutamate without compromising the flavor (Mouritsen et al., 2012, 2019a). The extracted amount of free glutamate did not change significantly with extraction temperatures above 60 °C and water hardness (Mouritsen et al., 2012, 2019a). All this information can be very useful for the interaction between scientists and chefs and for their joint work in phycogastronomy, not only the most popular species of edible seaweeds with an improved umami sensation are identified, but also the ideal conditions for efficient extraction of flavor.

The monosodium glutamate: benefits and safety

Although the glutamate occurs naturally not only in the edible seaweeds but also in many other food sources (e.g., cheese, meat, seafood, vegetables, etc.), monosodium glutamate (MSG) is frequently used in its pure form as a food flavor enhancer (Jinap and Hajeb, 2010; Fernstrom and Smriga, 2017). MSG is classified as a flavor enhancer, according to the International Numbering System, based on the European system of naming food additives defined by Codex Alimentarius World Health Organization, and Food and Agriculture Organization (Codex Alimentarius, 1989; Khoadjaeva et al., 2013; Cebi et al., 2018). The MSG is considered as one of the world's most extensively used food additives to increase food deliciousness (Wijayasekara and Wansapala, 2017). When MSG is added to food, NaCl level can be reduced, and thus it can have a major role in healthy nutrition because many people have a great interest in reducing the daily sodium intake. The salt-reduction effect of MSG could be used to make a low-sodium diet more palatable (Fuke and Shimizu, 1993). However use of MSG as a flavor enhancer has been a controversial subject and its safety has been studied intensively for many years (Henry-Unaeze, 2017). There are many arguments for and against the use of this compound in gastronomy in terms of safety for human consumption. Namely, some reactions associated with the monosodium glutamate are commonly known as MSG-symptom complex (headaches, numbness, flushing, tingling, palpitations, and drowsiness), but so far there is no strong evidence associating MSG and these symptoms. The US Food and Drug Administration (FDA), classify it as 'generally recognized as safe' (GRAS) and whenever it is added as an additive, it must be referred (E621) on the product label (Geha et al., 2000; Choudhury and Sarkar, 2017; Henry-Unaeze, 2017). Recently, the European Food Safety Authority (EFSA) established an acceptable daily intake level of 30 mg $(kg)^{-1}$ body weight (EFSA, 2017).

In the Roman Empire, a fermented fish condiments called "Garum", with a high concentration of MSG was used as a flavor enhancer (Smriga et al., 2010). Nowadays, it is well-known that many foods naturally contain MSG (e.g., seafood, cheese, tomato, mushrooms, etc.) (Ninomiya, 1998; Nakamura, 2011). Besides natural food ingredients, many flavor enhancers containing MSG, such as bouillon cubes, condiments, or similar products, are often used. The use of umami-rich ingredients improves the acceptability and palatability of food, and increase satiety and hedonic effects (Fuke and Shimizu, 1993; Yamaguchi, 1998; Yamaguchi and Ninomiya, 2000; Beauchamp, 2009; Masic and Yeomans, 2013, 2014; Ninomiya, 2015). The preference for the use of MSG as a flavor enhancer was also proved by many healthy infants who enjoyed more eating soup containing MSG than soup without this flavor enhancer (Vazquez et al., 1982; Beauchamp and Pearson, 1991). North American youngsters also rated higher flavor, savoriness, and taste of soup with added MSG (Okiyama and Beauchamp, 1998). Some studies have examined the potential usefulness of MSG supplementation to improve the nutrition of elderly patients (Yamamoto et al., 2009). A similar study conducted with French and Japanese elderly people showed that their nutrients intake was improved when MSG was added to soups, rice, or potatoes (Bellisle et al., 1991; Sasano et al., 2014; Ninomiya, 2015).

Concluding, it was found that the loss of umami taste can cause deterioration in overall health due to loss of appetite and weight (Sasano et al., 2015). Nevertheless, in general very little is known about the relationship between the savory tastes, MSG and salt, and eating behavior, i.e., appetite, and these areas merit further studies in more detail (Donaldson et al., 2009).

Metabolic pathways of umami taste

Structure and function of umami taste receptors

The umami taste receptor is a heterodimer, a member of G-protein coupled receptors (GPCRs), consisting of T1R1 and T1R3 proteins (Kunishima et al., 2000; Li et al., 2002; Lindemann et al., 2002; Nelson et al., 2002; Zhao et al., 2003; San Gabriel et al., 2005; Yasuo et al., 2008; Bachmanov et al., 2009; Jyotaki et al., 2009; Kinnamon, 2009; Li, 2009; Temussi, 2009; Mouritsen and Khandelia, 2012; Dang et al., 2014). Like all GPCRs, T1R1 and T1R3 have a seven helix TM (7TM) domain, and a large extracellular domain called the Venus flytrap (VFT), which contains the active site for the specific ligands (Section 4.2) (Fig. 2). The heterodimer complex T1R1/T1R3 is a receptor, activated *in vitro* by umami taste compounds (L-glutamate and L-aspartate) (Li et al., 2002; Nelson et al., 2002). Except for its specificity for umami ligands, the T1R1/T1R3 receptor can play a central role in food acceptance (Temussi, 2009).

Besides heterodimer T1R1/T1R3, two membrane receptors coupled to protein G, mGluR4 and mGluR1, are also selective for umami L-glutamate (Chaudhari et al., 2000, 2009; Kurihara, 2015). Both mGluR4 and mGluR1 are activated by L-glutamate but not by nucleotides. Calcium-sensing receptors enhance the intensity of umami taste, and they propounded the taste-enhancing character as the '*kokumi*' flavor (Maruyama et al., 2012). Nevertheless, future experiments should explore in detail the complexity of subjective human taste, providing greater insight into a perception of umami taste.

Mechanism of interaction between umami taste receptors and ligands

The interaction between umami ligands and the T1R1/T1R3 receptor is the base of the umami activity theory. To study the mechanism of interaction between umami ligands and the umami taste receptor, several peptides of different lengths (selected as the umami ligands), were docked to find the combination mode and the properties of the binding sites (Dang et al., 2014). The mechanism was simulated by docking modeling of T1R1/T1R3 (Dang et al., 2014). The molecular simulations show that two amino acids, Ser146 and Glu277, both in T1R3 protein, played significant roles in the synergism of the umami taste. The interaction between umami ligand-receptor complexes was enforced by hydrogen bonding, electrostatic and hydrophobic interactions. The model suggested that in the T1R1/T1R3 heterodimer, T1R1 protein is closed, whereas T1R3 has an open conformation. The computer-assisted method showed that the closed T1R1 receptor had the assistant function while leading T1R3 acted as a heterodimer. Binding sites of L-glutamate and L-aspartate played essential roles in the interactions between umami peptides and T1R1/T1R3 receptor. The umami peptides described in food with residue glutamate or aspartate at the C-terminal sequence, show higher umami potential (Dang et al., 2014). Small peptides and glutamate can stabilize the active (open) T1R3 by binding to the outer vestibule of the Venus flytrap (VFT) domain of the receptor (Fig. 2). The Raman and Profile-3D scores of the model confirmed that docking was a reliable technique for the studying of a binding site of the ligands. The mechanism could be quite similar to other taste receptors (Kim et al., 2015).

Recent investigations of the synergistic effects between umami peptides, MSG, and the T1R1/T1R3 receptor, were performed by a novel bivariate model (Zhang et al., 2008, 2017; Dang et al., 2019). The results revealed specific changes between umami peptides and umami taste receptor, upon the addition of MSG. Namely, the addition of MSG enlarged the size of the binding cavity of the T1R3 and caused small peptides to bind with T1R3 with lower docking energy (Dang et al., 2019). The results facilitate the understanding of the synergism and based on the novel methods new umami and umami-enhanced compounds can be discovered. Undoubtedly future research for interpreting the interaction with taste receptor responses and other physiological responses should be conducted.

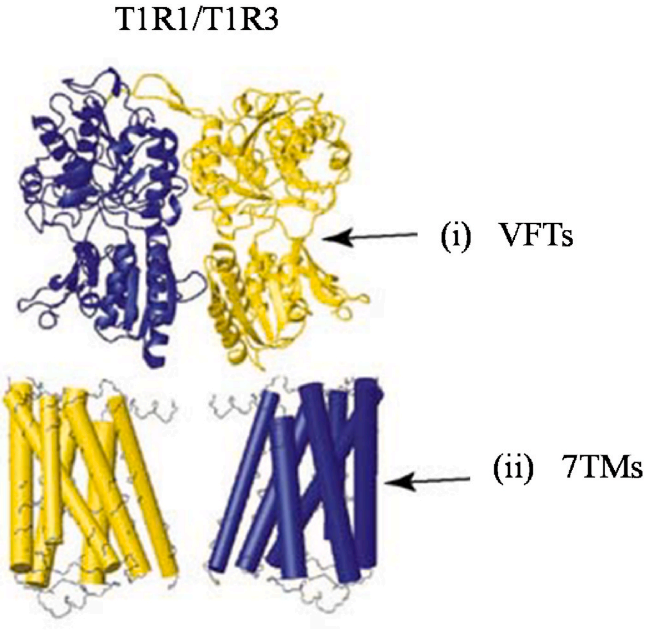

Fig. 2. Molecular models of umami taste receptors (adapted from Temussi, 2009). Generic models of heterodimeric umami T1R1/T1R3 receptor (T1R1 - blue; T1R3 - yellow). The molecular representation of the Venus flytrap (VFT) domains (i) of the T1R1/T1R3 heterodimer and the seven helix TM (7TM) domains (ii) are simplified and generated by MOLMOL (Koradi et al., 1996). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

Conclusions

The gastronomic potential of green, red, and brown edible seaweed species as umami flavoring agents, was reviewed. The concentration of the main umami compound, glutamate in extracts of seaweed species can vary in several orders of units, from very low (measured in few mg $(100\ g)^{-1}$) to very high (hundreds-thousands of mg $(100\ g)^{-1}$) in some red and brown species. This wide variation depends not only on seaweed species and their origins, but also on their storage and extraction procedure. However, despite the great availability and abundance (several hundred edible species), the free umami compounds were evaluated only for few species. Therefore, future research should pay more attention to these valuable umami food sources, to increase their beneficial application, particularly in Western cuisine.

Declaration of competing interest

The authors declare that there are no conflicts of interest.
(The recipes are available at the website of the 'Alga4Food') Blumenthal et al. (2009).

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