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Valorization of the chemical diversity of the tropical red seaweeds *Acanthophora* and *Kappaphycus* and their applications in aquaculture: A review

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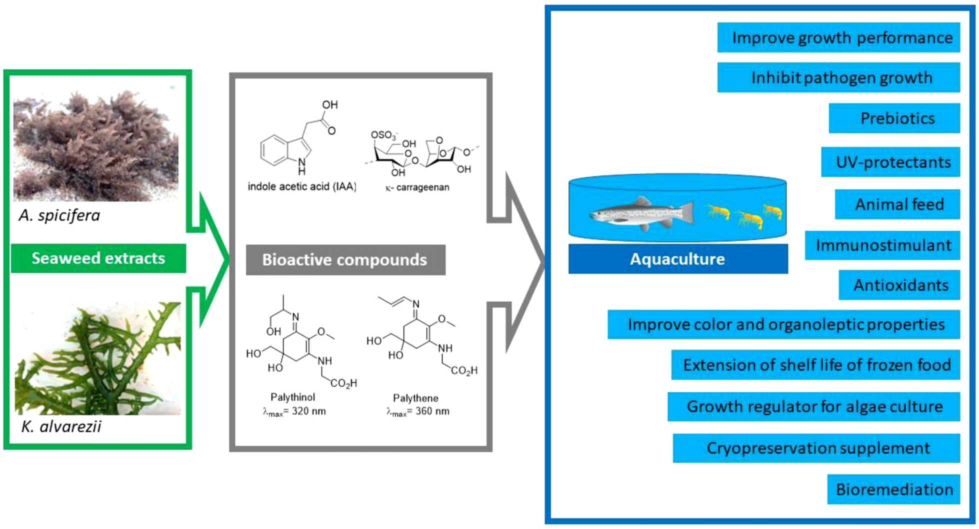
The role that seaweeds play as primary producers and ecosystems engineers in marine coastal ecosystems is widely acknowledged. Seaweeds, however, are also important drivers in the development of the blue bioeconomy due to their vast diversity of unique chemicals with a broad range of industrial and biotechnological applications. In tropical regions, seaweed production has been focused on a few species only, because of their hydrocolloids used in the food industry. There is a strong need to identify new applications of red seaweed species in other sectors such as aquaculture. Therefore, to diversify the culture of red seaweeds, more tropical species need to be investigated for their chemical composition and potential application in aquaculture, and then, to develop a method for a sustainable cultivation of new seaweed candidates and enhance their economic potential. Based on this context, we analyze the potential value of the red edible seaweed *Acanthophora* spp., an under-valued seaweed species which is naturally abundant in tropical countries, and *Kappaphycus* spp., a commercially valuable seaweed commonly used for polysaccharide extraction. The vast chemical diversity of seaweeds (polysaccharides, phytohormones, amino acids, and pigments) has led to research on a wide range of applications in aquaculture, including pathogen control, immunostimulant, antioxidant, bioremediation, feed, UV protectants, increase in seafood shelf life, animal colorant, and growth regulator for microalga culture. This review hopes to stimulate the interest among seaweed researchers to investigate other local seaweed species and seek greater added value of their biomass and chemical compounds and their applications in the aquaculture sector. Additionally, this information will help stakeholders to benefit from these two red seaweeds by contributing to the diversification of the blue bioeconomy in tropical countries.

KEYWORDS

Acanthophora, *Kappaphycus*, aquaculture, tropical seaweed, bioproduct, metabolites, blue economy, chemistry



GRAPHICAL ABSTRACT

1 Introduction

Seaweeds are photosynthetic and multicellular organisms commonly found in shallow coastal marine ecosystems. Seaweeds biosynthesize a wide range of natural products originating from different metabolic pathways (Cardozo et al., 2007) with a wide range of applications in food processing, pharmaceutical, nutraceutical and cosmetic industries as well in the agriculture and aquaculture sector. In recent years, the aquaculture sector has become more diverse and experienced an intensive growth around the world, especially in tropical regions (FAO, 2020). Seaweed cultivation has increased through the years around the world particularly in Asia (Naylor et al., 2021). *Kappaphycus* spp. and *Eucheuma* spp. have become the most cultivated species for carrageenan extraction, while other seaweeds, like *Undaria pinnatifida*, *Porphyra/Pyropia* spp., and *Caulerpa* spp., are being cultivated for human consumption. Recent studies have covered advances of seaweed nursery techniques and the importance to identify adequate environmental conditions for economically successful production in aquaculture systems (Hwang et al., 2022; Jiksing et al., 2022).

Seaweeds are also increasingly cultivated for bioremediation purposes in the aquaculture sector to help reducing the environmental impact, i.e. Integrated Multi-Trophic Aquaculture (IMTA) (Stévant et al., 2017). The implementation of land-based shrimp farms negatively impacts the environment causing eutrophication and polluting mangrove forest. The poor quality of water of shrimp farms can negatively affect growth of shrimp and increase the probabilities of shrimp disease outbreaks, which generate severe economic losses.

The incorporation of seaweeds into aquaculture systems has the potential to help the improvement of the marine ecosystem through their capacity to absorb nutrients from the water while synthesizing secondary metabolites with high-added value (Tanaka et al., 2020). IMTA cultivation of the kelp *Saccharina latissima* with the blue mussel *Mytilus edulis* improved the biomass of the kelp by 38%, reduced ephiphytes to 6% and increased the concentration of pigments such as chlorophyll *a*, fucoxanthin and phaeophytin, compared to monoculture (Hargrave et al., 2022). The seaweed *Chaetomorpha linum* cultivated in a IMTA system was found to be a prolific source of omega-3 and omega-6 fatty acids as a by-product of the bioremediation system (Stabili et al., 2019). Other seaweeds such as *Codium* and *Ulva* cultivated in land-based IMTA systems have shown to be alternative sources of commercially important polar lipids such as glycolipids, phospholipids, and betaine lipids (da Costa et al., 2015; Moreira et al., 2020), while IMTA cultures of *Gracilaria vermiculophylla* represent a promising source of photoprotective compounds known as mycosporine-like amino acids (MAAs) (Barceló-Villalobos et al., 2017). The chemical composition of seaweeds is highly variable when collected in the wild. Cultivation under control conditions through land-based IMTA systems presents an alternative to provide a continuous supply of compounds of commercial and nutritional interest.

One of the economically most significant and widespread cultivated seaweeds in tropical Asian countries is the red seaweed *Kappaphycus alvarezii*. Other countries, such as Mexico (Muñoz et al., 2004) and Brazil (Bulboa and De Paula, 2005), successfully cultivate introduced strains of *K. alvarezii* and *K. striatus*. This seaweed has also been introduced to other tropical regions around the world for mariculture including East Africa (Rönnbäck et al., 2002; Msuya, 2020) and the tropical Eastern Pacific (Hayashi et al., 2017).

Kappaphycus species are of interest for their high carrageenan content. Furthermore, among the three taxonomic groups of macroalgae; green (Chlorophyta), red (Rhodophyta) and brown (Ochrophyta and Phaeophyceae), red seaweeds are characterized by being the most important source of bioactive metabolites with higher protein content and for being the group with higher species diversity in the tropical eastern pacific (TEP) (Cortés et al., 2017). Additionally, the presence of abundant biomass of other red seaweed species in the coast of tropical countries should also be considered for their investigation and potential applications of their biomass and chemical constituents along with the ecology and social economic impact. For example, the red seaweed *Acanthophora* spp., is found abundantly in the wild, but its potential applications in different sectors is still to be evaluated.

Acanthophora is commonly found in tropical, marine ecosystems. *Acanthophora spicifera* has been considered as the most widespread and invasive species reported in the Eastern Pacific Ocean (Ávila et al., 2012). Its morphological plasticity, high capacity to adapt to different environmental conditions and its capacity to reproduce vía sexual or vegetative reproduction, makes it a threat to native marine biodiversity. *A. spicifera* can grow on different types of substrate such as rocky, sandy, shells, concrete and buoys exposed to diverse physical and environmental parameters such as water movement, light, salinity, and water temperature that have strong influence in its propagation (Russell, 1992). Harvesting the biomass of *A. spicifera* from the natural environment might be a way to reach two goals: (1) conservation of the natural marine environment with respect to control of invasive seaweed species and (2) developing a local bioeconomy by valorizing the harvested biomass. Although there is a scarce information about the ecological impact of *Acanthophora* spp. on native species in tropical region, a study carried out in Hawaii demonstrated that *Acanthophora spicifera* did not have a negative effect on epifaunal distribution (Fukunaga et al., 2014).

Even though, the ecological impact of invasive seaweed species should be carefully considered in all marine ecosystems, chemical characterization and valorizing its potential industrial applications could be worth it. For example, the presence of high feedstock of invasive seaweed species in the Iberian Peninsula (Pacheco et al., 2020) and the coast of Spain (Pereira et al., 2021) were reported and evaluated for their potential applications in different industries, suggesting their use as an alternative to decrease their population while achieving environmental and economic benefits. However, other seaweed such as *Undaria pinnatifida*, which is considered an invasive species in several countries such as France, Ireland and New Zealand (Kraan, 2017), but cultivation permits have been granted by local authorities to cultivate the species due to its economic potential in the food industry.

In this study, we analyze the potential use of the biomass and the chemical constituents, such as polysaccharides, pigments, amino acids, and peptides, and phytohormones of two tropical red seaweed species *Kappaphycus* and *Acanthophora* and their high value-added applications in the aquaculture sector.

2 General characteristics

2.1 *Kappaphycus* spp.

The commonly cultured *Kappaphycus* strains have been extensively introduced to various tropical countries as a source of carrageenan for the food industry (Ask and Azanza, 2002; Zuccarello et al., 2006). The genus *Kappaphycus* is comprised of five taxonomically accepted species: *K. alvarezii*, *K. inermis*, *K. malesianus*, *K. procrusteanus* and *K. striatus* (Dumilag et al., 2022). *K. alvarezii* includes three strains (red, green, and brown) and has been widely studied for their growth rate and carrageenan yield (Muñoz et al., 2004). There is a long list of cultivars of different *Kappaphycus* spp. For example, in the Phillipines over 60 different cultivars have been investigated (Dumilag et al., 2022). Recent studies have focused on the germination of tetraspores and carpospores from wild, harvested *K. alvarezii* (Hinaloc and Roleda, 2021).

Temperature is the most important factor that determines the growth rate in *K. alvarezii* and *K. striatus* (Muñoz et al., 2004; Bulboa and De Paula, 2005). Both species have shown higher growth rates during warm seasons but limited growth below 18°C for longer periods. Although *K. striatus* has shown a good growth rate and carrageenan yield, the presence of viable tetraspores during *in vitro* and in the sea experiments under different light and temperature conditions, suggest considering only *K. alvarezii* for commercial cultivation purposes to prevent propagation and possible environmental damage (Bulboa and De Paula, 2005). However, the negative impact caused by *K. alvarezii* on the coral *Acropora* sp., and bleaching of the fire coral *Millepora alcicornis* was reported in India (Chandrasekaran et al., 2008) and Venezuela (Barrios et al., 2007) respectively. Therefore, cultivation near biodiverse ecosystems should be highly reconsidered. Analysis of farming techniques based on biotechnological tools, ecological interactions and the challenges involved in *K. alvarezii* culture has been reviewed (Bindu and Levine, 2011). To increase the economic viability, sequential extractions of the same biomass of *K. alvarezii* to obtain carrageenan, chlorophyll, β-carotene, essential amino acids and phytohormones have been suggested for a green biorefinery development (Rudke et al., 2020). Several investigations have been focused on improving biomass cultivation methods of *Kappaphycus* as a monoculture such as micropropagation (Rama et al., 2018; Ali et al., 2020), culture on biofloc effluents (Pires et al., 2021), tissue culture (Budiyanto and Abadi, 2019), or as part of an IMTA using different systems like floating bamboo raft (Mantri et al., 2022), tubular net (Reis et al., 2015; Periyasamy and Subba Rao, 2017), floating cages and longlines (Mustafa, 2017), and stratified double net rounded cage (Putro et al., 2015).

The proximal composition of *Kappaphycus* species have been reported in different studies (Table 1).

2.2 *Acanthophora* spp.

The genus *Acanthophora* is currently composed of 7 accepted species according to Algaebase (Guiry and Guiry, 2022): *A. spicifera*, *A. muscoides*, *A. aokii*, *A. dendroides*, *A. nayadiformis*, *A. pacifica* and *A. ramulosa*. Although, most species are restricted to tropical regions, some species such as *A. spicifera* and *A. muscoides* extend into temperate regions (Jong et al., 1999).

The presence of *A. spicifera* in mangrove ecosystems and results of experimental studies, indicate the species can grow under a large salinity range (25 to 40 g/100 g water) (Cordeiro-Marino et al., 1992; Pereira et al., 2017). Up till now, no studies on this seaweed biomass production in mangrove ecosystems have been recorded to evaluate its sustainable production.

Morphological changes, such as increased cell wall thickness and chloroplast disruption, reduced cell viability and growth rate, were also observed in *A. spicifera* after exposure to UV-B radiation which increases the formation of reactive oxygen species (ROS) within the cell (Pereira et al., 2017). Stress response was more obvious when plants were cultivated under higher salinity conditions. When *A. spicifera* was exposed to UV radiation in combination with higher nutrient availability, a reduction on these negative effects was observed. The fact that increased nutrient concentration can offset the negative effects of UV radiation could be explained by the capacity of the seaweed to incorporate nutrients that transform through different metabolic pathways into specific UV-absorbing compounds such as mycosporine-like amino acids (Häder et al., 2015).

The proximal composition of *Acanthophora* species have been reported (Table 2).

3 Seaweed biomass with applications in aquaculture

3.1 *Kappaphycus* spp.

Aquaculture applications of *Kappaphycus* spp. are numerous. They include biomass cultivation, bioremediation, and animal feed production.

The economic and environmental benefits of culturing *Kappaphycus* species with commercially important aquatic animals in diverse IMTA systems has been investigated in several studies (Qian et al., 1996; Lombardi et al., 2006; Rodriguez and Montaño, 2007; Hayashi et al., 2008; Putro

TABLE 1 Proximal composition of *Kappaphycus* spp.

Parameter(g/100 g dw)*	*K. alvarezii*	*K. striatus*	*K. malesianus*	*K. inermis*
Lipids	0.03-1.50 [a,b,c,d,e,f,g,h,i,j]	0.06-0.08 [c,f]	**	**
Protein content	1.03-18.16 [a,b,c,d,e,f,g,h,i,j]	0.73-1.25 [c,f,g]	**	**
Carbohydrate content	8.67-71.83 [b,c,d,g,h,i,j,l]	5.15-8.35 [c,f,g]	**	**
Sulfated polysaccharide content	6-67.30 [a,e,m,n,o,p,q]	30-56.40 [n,p,r]	37 [p]	29 [n]
Ash content	5.01-45.37 [a,b,c,d,e,f,g,h,k]	4.80-35.88 [c,f,g]	**	**
Fiber	0.87-34.09 [a,b,c,f,g,j,k,l]	1.18-15.81 [c,g]	**	**

*Ranges of all values found in literature
[a](Hurtado, 1995); [b] (Hong et al., 2007); [c] (Balasubramaniam et al., 2013); [d] (Suresh Kumar et al., 2015); [e] (Yong et al., 2014); [f] (Ariano et al., 2021); [g] (Adharini et al., 2019); [h] (Alcantara and Lazaro-Llanos, 2020); [i] (Abirami and Kowsalya, 2011); [j] (Kumar et al., 2014); [k] (Xiren and Aminah, 2017); [l] (Fayaz et al., 2005); [m] (Castelar et al., 2016); [n] (Santos, 1989); [o] (Estevez et al., 2000); [p] (Bui et al., 2019); [q] (Ohno et al., 1994); [r] (Hung and Trinh, 2021).
** No scientific information available.

et al., 2015; Kambey et al., 2020; da Silva et al., 2022). In those studies, the productivity of the cultivated species in open water and land-based systems was increased supporting IMTA technology as a viable method for seaweed production. These systems provide a sustainable method for the development of the aquaculture industry with ecological benefits, especially in developing countries. For example, an improved growth rate of *K. alvarezii* and the pearl oyster *Pinctada martensi* was observed in a co-culture system established in a subtidal zone in the coast of Hainan Island in China. Both organisms showed higher growth rates when seawater temperature was over 23°C, due to the efficient nutrient uptake by *K. alvarezii* removing nitrogen waste, particularly ammonium, and improved seawater quality (Qian et al., 1996). Although, *K. alvarezii*, *K. striatum* and *Kappaphycus* sp., all significantly reduced the ammonium concentration in fish farm effluent, *K. striatum* showed the best performance compared to the two other species (Rodriguez and Montaño, 2007). Also, the growth of *K. striatum* improved the growth rate of the sea cucumber *Holothuria scabra* in a co-culture system established in a tropical lagoon in Tanzania (Beltran-Gutierrez et al., 2016). The implementation of integrated aquaculture systems in lagoons, represents an alternative for the economic development in this area, particularly in countries where space for marine aquaculture is a limitation. Additionally, alternative methods to improve seaweed biomass production by increasing its resistance to diseases without affecting its polysaccharide quality have been reported. For example, a short immersion (12 hours) of *K. alvarezii* in a high nitrogen medium enhanced the growth, nitrogen uptake, and carrageenan quality and reduced the incidence of the "ice-ice" disease during its cultivation in the sea for 45 days (Luhan et al., 2015). Furthermore, the use of a bioflocs system with effluents released from farming of white Pacific shrimp (*L. vannamei*) improved the growth and biosynthesis of secondary metabolites with antioxidant activity, such as phenolics, carotenoids and flavonoids, during *in vitro* cultivation of *K. alvarezii* (Pedra et al., 2017).

From a bioremediation point of view, *K. alvarezii* was capable of removing 23–34% of ammonium and 5–30% of phosphate after 42 days of cultivation using seaweed biomass inside a fish cage system (Kambey et al., 2020). The dried biomass of *K. alvarezii* also showed high biosorption capacity for the removal of phosphate and heavy metals (Pb^{2+}, Cu^{2+}, Fe^{2+} and Zn^{2+}) from contaminated waters (Rathod et al., 2014; Rahman and Sathasivam, 2015) and under laboratory conditions (Lee et al., 2011). The *K. alvarezii* brown strain showed higher biosorption of cadmium, cobalt, and chromium with values of 3.064, 3.365 and 2.799 mg/100 g fresh weight respectively, compared to the red and pale yellow strains during the experiments undertaken in the laboratory (Kumar et al., 2007).

Additionally, *K. alvarezii* biomass and its extracts have been included in animal feed and to improve the physiological and immunological response in economic important aquaculture species. The nutritional composition and low heavy metal content in *K. alvarezii* and *K. striatus* suggest their use for animal feed (Ariano et al., 2021). Supplementing with 15 g of seaweed/kg feed, resulted in a 10% increase in the survival rate of the white Pacific shrimp *L. vannamei* in a *Vibrio harveyi* challenge test (Suantika et al., 2018) (Table 3). *K. alvarezii*-enriched artemia used to feed the white shrimp *L. vannamei* increased the resistance against *V. harveyi* during the post-larvae phase and improved shrimp growth in a high-salinity environment (Suantika et al., 2017). The amino acid and fatty acid content increased through the fermentation of *K. alvarezii* with 10% of activated *Saccharomyces cerevisiae* provided a better alternative as a feed supplement for the white shrimp compared to the non-fermented one (Hardjani et al., 2017). Other studies demonstrated that higher lipid content improved the growth and survival rate and enhanced the larval immune system and stress tolerance in shrimps (Zhang et al., 2013; Xie et al., 2018). The use of raw and fermented *K. alvarezii* in the diet of up to 10 and 30%, respectively, for the feed of freshwater prawn *Macrobrachium rosenbergi* increased growth rate, protein and lipid digestibility and feed utilization efficiency (Felix and Brindo, 2014). The use of up to 5% of *K. alvarezii* as a binder in shrimp food to improve the survival rate of *Penaeus monodon* and to reduce organic waste generated by commonly used binder ingredients, such as wheat flour, has been suggested over 25 years ago (Peñaflorida and Golez, 1996). Also, higher growth rate and weight gain of the

TABLE 2 Proximal composition of *Acanthophora* species.

Parameter* (g/100 g dw)	*A. spicifera*	*A. nayadiformis*	*A. muscoides*
Lipids	0.30-5.43 [a,b,c,d,e,f,g,h,i]	0.29-2.19 [j]	**
Protein content	5.29-20.59 [a,b,c,d,e,h,i,]	1.71-3.15 [j]	21.83[k]
Carbohydrate content	26.20-88.26 [a,b]	**	**
Sulfated polysaccharide content	9.1-39.3 [l,m,n]	**	**
Ash content	14.80-47.04 [a,c,d,e,h]	**	**

* Ranges of all values found in literature
[a] (Herrera et al., 2019); [b] (Abomohra et al., 2018); [c] (Kailas and Nair, 2015); [d] (Dixit et al., 2018); [e] (Lawanyawut et al., 2002); [f] (Bhaskar et al., 2004); [g] (Marolia et al., 1982); [h] (Ganesan et al., 2020); [i] (Seenivasan et al., 2012); [j] (Polat and Ozogul, 2008); [k] (Rao, 1970); [l] (Schnoller et al., 2020); [m] (Anand et al., 2018); [n] (Ganesan et al., 2018);
** No scientific information available.

TABLE 3 Overview of aquaculture growth and pathogen challenge tests.

Parameter	*K. alvarezii*[a]	*K. alvarezii*[b]	*A. spicifera*[c]
Preparation type	*Artemia nauplii* enriched with seaweed paste (0.5 g/L *artemia* enrichment suspension)	Mixture of seaweed powder and *Artemia nauplii* (15 g/kg feed)	Mixture of seaweed extract and lab-prepared feed
Animal used	*L. vannamei (post-larvae)*	*L. vannamei (nursery phase)*	*C. punctatus*
Growth rate after challenge: control (% body weight/day)	9.65 ± 0.20	6.49 ± 1.84	
Growth Rate* after challenge: seaweed (% bwt/day)	10.51 ± 0.19	6.56 ± 2.28	
Pathogen	*Vibrio harveyi*	*Vibrio harveyi*	*Aeromonas hydrophila*
Survival rate after challenge: control(%)	77.7 ± 3.1	63.8 ± 1.6	0
Survival rate after challenge: seaweed(%)	90.2 ± 7.0	73.3 ± 1.6	60

[a] (Suantika et al., 2017); [b] (Suantika et al., 2018); [c] (Muthukrishnan and Raja, 2021).

seabass *Later calcarifer* was observed when supplemented with 6% of cooked *K. alvarezii* in its diet (Shapawi et al., 2015).

Interesting applications of *Kappaphycus* spp. extract (sap) in aquaculture have been reported with potential benefits for the industry. The use of the sap as a feed supplement for the commercial shrimp *Penaeus monodon* improved the survival from 73.7% (control) to 89.7% (treatment) (Anil et al., 2011). In addition, *K. alvarezii* ethyl acetate extract displayed inhibitory activity against *Vibrio harveyi*, one of the most important pathogens in the shrimp industry (Sivakumar et al., 2014). Although, some compounds, such as fatty acids and hydrocarbons, were identified through GC-MS analysis, further studies to isolate and characterize the bioactive compounds present in this extract and other types of extracts are required. Furthermore, the *K. alvarezii* methanolic extract showed an anti-genotoxic activity in the marine fish *Therapon jarbua* (Nagarani et al., 2012). The DNA damage in the fish was induced by exposure to mercury chloride, but after addition of the extract of this seaweed of up to 5 mg/L of tank water, DNA damage was notably reduced.

3.2 *Acanthophora* spp.

Aquaculture applications of *Acanthophora* spp. are numerous. They include biomass cultivation and animal feed production and the extension of shelf life of food.

Cultivation of *Acanthophora* was accomplished using 5 cm vegetative fragments, tied to polypropylene straws and fixed to nylon fishing lines at 1m depth in the nearshore area of Gulf of Mannar, India. An 2.6-fold increase of the initial weight (4.85 kg) was noted after 25 days from cultivation with a harvest weight of 12.85 kg (Kaliaperumal et al., 1987). However, no studies using *Acanthophora* in IMTA systems have been reported in the literature.

Acanthophora species are a rich source of carbohydrates, lipids, proteins, minerals, fatty acids, essential amino acids, and bioactive compounds (Table 2) that could be used for aquatic animals as a functional feed to enhance their growth, increase survival rate, protection against diverse pathogens or as a mechanism of chemical defense (Lawanyawut et al., 2002). Another reason is to reduce the use of animal-based protein in animal feed and the feed production costs (if collected seaweeds are being used). In natural ecosystems, this seaweed is an important natural food source for aquatic animals such as the green turtle *Chelonia mydas* L. (Russell and Balazs, 1994) and the blue striped angelfish *Chaetodontoplus septentrionalis* (Leu et al., 2010).

The shrimp industry is one of the most important economic sectors in tropical and subtropical countries. However, increasing shrimp farming has resulted in negative environmental impacts caused by pollution of mangrove forest and the nutrient enrichment of seawater. The use of *Acanthophora* species as bioindicators in shrimp farms and natural habitats in the vicinity of shrimp farms is an interesting alternative to reduce the ecological and environmental impact generated by the presence of the excessive nutrient concentration in the sea. This is because this excessive nutrient concentration in the sea leads to an increased presence of *Acanthophora* sp. In fact, the growth, N content in tissue and $\delta^{15}N$ values in *A. spicifera* were used as a bioindicator in commercial shrimp farms (Lin and Fong, 2008). The growth and tissue N content was found to be higher in the sample collected closer to shrimp farming than those obtained at further distances. Additionally, analyzing isotopic ratios is a very sensitive technique that could be applied to detect effluent effects at very distant places and determine the main nutrient source in a specific location of a marine ecosystem. The increase in the growth and higher absorption of phosphorus by *A. muscoides* in a high salinity environment was evidenced by

(Tanaka et al., 2020). Concentration of UV-absorbing metabolites with maximal UV absorption at 331 nm was highest when grown at normal salinity. The considerable capacity of the seaweed to absorb and store nutrients and use them for growth and to produce a wide diversity of chemicals could be used as additional material for the elaboration of high-added value bioproducts.

Some studies have reported on the bioactivity of *Acanthophora* crude extracts in aquaculture. For example, the aqueous extract of *A. spicifera* displayed immunostimulant activity against the fish pathogen *Aeromona hydrophila* providing a survival rate of 60% of the striped murrel *Channa punctatus* compared to 0% survival rate of the control group (Muthukrishnan and Raja, 2021).

Feeding studies of *A. muscoides* in the juvenile top shell *Trochus niloticus* showed a daily growth rate of 0.022 mm in diameter and 6 mg in wet weight, while the control group slightly decreased its weight daily (Lee and Amos, 1997).

Another reported application is the extension of the shelf life of frozen stored shrimp after being treated with a 5% ethanolic extract of *A. muscoides* (Arulkumar et al., 2020). A reduction of the formation of toxic biogenic amines in shrimp demonstrated the biopreservative potential of this red seaweed. The presence of diverse metabolites with antioxidant activity in *Acanthophora* (Zakaria et al., 2011; Dixit et al., 2018), contributes to preventing food lipid peroxidation and therefore its potential use as natural source of antioxidants.

4 Bioactive metabolites with applications in aquaculture

4.1 Polysaccharides

Hydrocolloids are high-molecular weight polysaccharides with unique physicochemical properties including gelling, thickening, and emulsifying at determined thermal conditions (Gupta and Raghava, 2008). Red seaweeds are the only source of carrageenans, and agars, two of the most economically important polysaccharides (phycolloids) characterized by their diverse rheological properties with different industrial applications. The structural diversity of carrageenan and agar have been reviewed (Usov, 2011; Ciancia et al., 2020).

A comprehensive review by (Mohan et al., 2019) describes the wide range of potential applications of marine-derived polysaccharides in aquaculture such as feeding, immunostimulant, antioxidant, antiviral, antifungal, antiparasitic and antibacterial activity. The different physico-chemical properties, biodegradability, non-toxicity, biocompatibility, and diverse biological activities make seaweed polysaccharides a promising source for the discovery of novel applications in the aquaculture sector. Therefore, it is important to characterize the chemical composition of other native and non-indigenous seaweeds, especially characterize their chemical composition and phycolloid content to enhance their potential use in aquaculture.

In addition, the chemical or enzymatic hydrolysis of seaweed polysaccharides will lead to the production of bioactive oligosaccharides with multiple pharmacological and cosmeceutical applications (Cheong et al., 2018). The biological activity displayed by oligosaccharides is dependent on the degree of depolymerization of the polysaccharide of origin. In aquaculture, oligosaccharides have also shown beneficial results for their capacity to improve the productivity, their antibacterial activity, and as efficient prebiotics (Sardari and Nordberg, 2018). The application of 0.5 and 1% of mannan oligosaccharides (commonly found in yeast) in the diet of the Thinlip grey mullet (*Liza ramada*) showed an enhanced specific growth rate of 2.57 and 2.54%/day, respectively, compared to the control (2.34%/day). Also, an increase of the digestive enzyme activity, such as lipase, amylase and protease, blood immunity and antioxidant activity, were observed (Magouz et al., 2021).

4.1.1 *Kappaphycus* spp.

The sulfated polysaccharide κ-carrageenan is the major cell wall component in *K. alvarezii* (Santos, 1989; Hurtado, 1995) and its presence has also been reported in *K. inerme*, *K. striatus* (Santos, 1989; Mendoza et al., 2002) and *K. cottonii* (Santos, 1989). However, very small amounts of ι-carrageenan and agaroids were also found in *K. alvarezii* when extracted at room temperature (Estevez et al., 2000). Furthermore, other polysaccharides, such as β-(1,4)-ᴅ-glucomannan and β-(1,4/1,3)-ᴅ-glucan 6-sulfate, have also been found in the latter (Lechat et al., 2000). *K. alvarezii* is one of the most widely cultivated seaweeds in the world for the extraction of κ-carrageenan which has an important economic value in the food industry, but it has also shown promising applications in the pharmaceutical industry for its wide range of biological activities or as a biomaterial for drug delivery systems (Cunha and Grenha, 2016; Hentati et al., 2020). Although very few studies have focused on the potential application of *K. alvarezii* polysaccharides in aquaculture, the use of different marine-derived polysaccharides as binders for feeding (Paolucci et al., 2015), as growth promoters, immunomodulators, to induce disease resistance and gut health maintenance or as immunostimulants have been reported (Mohan et al., 2019). In fact, κ-carrageenan induces immunostimulatory activity, enhances growth and resistance to diseases in the Asia seabass *Lates calcarifer* (Sakthivel et al., 2015) and postlarvae of tiger shrimp *P. monodon* (Jumah et al., 2020).

4.1.2 *Acanthophora* spp.

Studies have also been carried out to determine the hydrocolloid composition of *Acanthophora* species, with *A. spicifera* being the most studied species. Some of these studies demonstrated that the sulfated galactan λ-carrageenan is the major polysaccharide present in *A. spicifera* (Parekh et al., 1989; Gomaa and Elshoubaky, 2016; Anand et al., 2018). However, other authors reported the presence of agar as major component in the polysaccharide extracts of *A. spicifera* (Gonçalves et al., 2002; Duarte et al., 2004; Schnoller et al., 2020; Júnior et al., 2021) and *A. muscoides* (Rodrigues et al., 2016a).

Various factors, including geographical location, the different environmental conditions or potentially the presence of cryptic seaweeds, can potentially explain the variation in the major polysaccharide constituent of *A. spicifera*. Interestingly, the phycolloids reported from Brazil and Mexico corresponded to the agaran type, while the carrageenan types are reported from the Indian Ocean (India and Saudi Arabia). Further studies are required on the genetic diversity and structural analysis of phycolloids of *Acanthophora* specimens from various locations to investigate the underlying variation in cell wall characteristics.

An unidentified sulfated polysaccharide from *A. muscoides* was used, due to its antioxidant properties, to evaluate its performance in semen cryopreservation of the commercial fish *Colossoma macropomum* (tambaqui) (Pereira et al., 2020). Although, no significant difference in the improvement of semen quality was found when *A. muscoides* polysaccharide was added as a supplement in the cryopreservation medium, the author concluded that further studies were required to exploit its potential as a supplement for semen cryopreservation of the most commercially important fishes. Since the antioxidant activity displayed by seaweed polysaccharides varies depending on the season and geographical location of the collected sample, more studies should be carried out to determine the best spatial and temporal conditions when maximum antioxidant activity is displayed. Also, it is important for future studies on the antioxidant and total phenolic content assays from seaweeds to have a standardized methodology for these analysis. Currently, there are different methodologies used by several researchers that makes it very complicated to compare the data with the reported literature.

4.1.3 Potential based on results of other species

No studies have been reported on the application of oligosaccharides from *Acanthophora* and *Kappaphycus* in aquaculture. However, methodological studies to optimize isolation of oligosaccharides from *K. alvarezii* (Bouanati et al., 2020), *K. striatus* (Yu et al., 2017), *A. spicifera* (Duarte et al., 2004) and *A. muscoides* (Rodrigues et al., 2016b) are available. Therefore, it is important to investigate and evaluate the potential application of polysaccharides and oligosaccharides isolated from *Acanthophora* and *Kappaphycus* in aquaculture, based on the different uses of these chemical compounds obtained from other seaweeds.

The different physico-chemical properties displayed by polysaccharides shows potential use in the development of matrices for vaccine micro-encapsulation (Borgogna et al., 2011), functional bio-composites (Paolucci et al., 2015), prebiotics (Vidhya Hindu et al., 2019), and anti-biofilm agent (Zammuto et al., 2022) for aquaculture purposes. In fact, *Artemia nauplii* encapsulated with the unidentified crude polysaccharide of the red seaweed *Amphiroa fragilissima* for the feeding of the shrimp *Litopenaeus vannamei* enhanced its growth, biochemical composition, digestive enzyme activities and antioxidant properties which led to the improvement of larval quality (Muttharasi et al., 2021). Furthermore, the application of agar-based pellets in the feeding of the sea urchin *Paracentrotus lividus* showed higher water stability in water recirculating system and was easily consumed by the animal without affecting its gonad growth (Fabbrocini et al., 2012).

Also, the immunostimulant, antibacterial and antiviral activity reported for seaweed polysaccharides, enhances their use as a natural and environmentally friendly alternative to treat and control several diseases affecting fish, shrimp cultivation and other organisms produced through aquaculture (Marudhupandi and Inbakandan, 2015; Rizzo et al., 2017; Raguraman et al., 2020). An increased immunological response, upregulation of immune-related genes and resistance to pathogens was reported through *in vitro* and *in vivo* studies after the shrimp *L. vannamei* was exposed to λ-carrageenan *via* immersion and orally (Chen et al., 2014). It is suggested that carrageenan triggers shrimp innate immunity and improves immune parameters such as haemolymph sampling, haemocyte counts, phenoloxidase (PO), respiratory burst (RBs), superoxide dismutase (SOD) and lysozyme activity.

For years, the brine shrimp *Artemia* and the microalgae *Chlorella* have been traditionally used as a food source in the shrimp industry. Many investigations intended to improve the nutritional characteristics that could enhance shrimp's survival at the different stages of their life cycle. For example, micro-encapsulated, micro-bound and micro-coated diets have been prepared with different nutrients depending on the nutritional requirements of the shrimp or larvae and evaluated for their capacity to increase the productivity and health (Kanazawa, 1989). In the formulation of this micro-bound diet for shrimps, κ-carrageenan has been used as a binder and showed an improvement on the survival rate and growth of shrimp's larvae and post-larval stages when it was combined with *Artemia salina* (Bautista et al., 1989). Other studies showed a boost in the immunological response of shrimps and fishes when supplemented with κ-carrageenan in their diet. An improved immunological activity and pathogen resistance of *L. vannamei* against the *infectious myonecrosis virus* (IMNV) (Febriani and Nuryati, 2013) and of *P. monodon* against *Vibrio harveyi*

(Traifalgar et al., 2013) were reported after feeding at 1.5% and 0.2% of κ-carrageenan, respectively. An improved growth, survival rate and immunological response of the Nile tilapia *Oreochromis niloticus* was observed by increasing the expression of immune-related genes including transferrin, IL-1β and appetite-related gene GH after administration of 0.5% of κ-carrageenan (Villamil et al., 2019). Similar results were reported with cobia *Rachycentron canadum* after feeding with 20 g/kg of κ-carrageenan (Harikrishnan et al., 2021). On the other hand, (Mariot et al., 2021) did not find significant difference in shrimp immunological response upon addition of up to 1.5% of κ-carrageenan to their diet. However, a small variation was noticed in the gut bacterial composition in a dose-dependent manner to carrageenan. Two unidentified bacteria of the families Rhodobacteraceae and Caldilineaceae with two bacteria of the family Rubritaleaceae were found in higher abundance when the concentration of κ-carrageenan was increased along with the shrimp resistance to White Spot Syndrome Virus (WSSV) disease. Recent studies have shown improvement in the metabolism of the white shrimp *L. vannamei* using the seaweeds *Ulva lactuca* and *Eisenia* sp., which increases the digestive enzymatic activity and variation in the gut microbiota while reducing the presence of pathogenic bacteria (Schleder et al., 2020; Omont et al., 2021). The prebiotic potential of marine polysaccharides and oligosaccharides has been recently reviewed (Gurpilhares et al., 2019; Zheng et al., 2020). The elicitor activity displayed by oligosaccharides provides a natural alternative to reduce disease outbreaks and improve the cultivation of seaweeds in aquaculture. The application of synthetic oligoagar at 100 µg/mL for 2 hours during the cultivation of the seaweed *Pyropia haitanensis* improved the seaweed growth, oxygen consumption and enhanced the upregulation of defense-related genes (Chen et al., 2016) and triggered oxidative burst releasing hydrogen peroxide in seaweeds such as *Gracilaria* spp. (Weinberger and Friedlander, 2000) and *Laminaria digitata* (Kupper et al., 2001), among others. Seaweed oligosaccharides have been studied for their use in the agriculture, medical and food industry (Zhu et al., 2021), however, their use in aquaculture as natural elicitors and as prebiotic remains to be exploited.

4.2 Phytohormones

Phytohormones, such as auxins, cytokinins, polyamines, abscisic acid, betaines, and gibberellins, are well known as plant growth regulators. These molecules are involved in important physiological functions such as mediating growth, signaling environmental alterations, initiating biotic or abiotic stress response and as indicator molecules during plant growth (Shanab and Shalaby, 2021). In seaweeds, phytohormones control different biochemical and physiological processes (Tarakhovskaya et al., 2007) and the mechanism of action of certain phytohormones such as indole acetic acid (IAA), N6-(Δ2-isopentenyl) adenine (iP), and abscisic acid in red seaweeds is suggested to be different from those reported from terrestrial plants (Mikami et al., 2016). Although, the presence of these molecules in red seaweeds (Yokoya et al., 2010; Wang et al., 2014), and the diverse extraction methods used (Górka and Wieczorek, 2017; Mori et al., 2017; Mohanty and Adhikary, 2018) have been reported in the literature, there are very limited studies on their identification and quantification in *Kappaphycus* and *Acanthophora* species and their application in aquaculture.

4.2.1 *Kappaphycus* spp.

The content of growth-hormone regulators in organic extracts and saps of *K. alvarezii* has been reported (Zodape et al., 2009; Prasad et al., 2010; Sedayu and Basmal, 2013; Layek et al., 2015; Fadilah et al., 2016; Cokrowati et al., 2021; Trivedi et al., 2022). In those studies, the presence of auxins such as indole-3-acetic acid (IAA), gibberellic acid (GA_3, GA_7), cytokinins (cis-zeatin, trans-zeatin, kinetin), choline, glycine betaine and betaine aldehyde have been found at different concentrations (Table 4). Two key factors in their quantification are: (1) the different extraction methods and solvents used for phytohormone extraction, and (2) the seaweed collection time and location. Nevertheless, the application of these hormones has been widely used to improve the biomass growth, photosynthesis and chemical composition of seaweeds including *Kappaphycus* species. Higher auxin content (16.28 mg/kg fresh weight) was found in the young thallus of *K. alvarezii* green strain from Indonesia compared to the old thallus of the green and brown strains (Cokrowati et al., 2021). The concentration of phytohormones present in *K. alvarezii* sap was determined by comparing three different methodologies, being spectrophotometric, HPLC, and ESI-MS (Prasad et al., 2010). The values obtained through ESI-MS analysis are more reliable than the other methodologies, since the interference caused by impurities is significantly reduced by their identification through their MS fingerprint.

For cultivation purposes, these plant growth regulators have been used alone or in combination to improve strains of *K. alvarezii* and increase the stock production through micropropagation. In addition, it has been proven that colchicine inhibits spindle fibers formation during cell division. The production of new strains using colchicine alone or in combination with phytohormones has potential to enhance micropropagation of seaweeds (Hayashi et al., 2007). Earlier studies demonstrated the efficacy of the use of phytohormones in enriched media to enhance branch culturing, reduce epiphyte contamination, improve daily growth rate and regenerate callus of *K. alvarezii* for micropropagation (Dawes and Koch, 1991; Dawes et al., 1993; Dawes et al., 1994; Hurtado and Biter, 2007). An improved callus induction of *K. alvarezii* with the plant growth regulators 1-naphthaleneacetic acid (NAA) and 6-

TABLE 4 Phytohormone content in *A. spicifera* and *K. alvarezii*..

Parameter *	***A. spicifera*** **(µg/g fresh weight)**	***K. alvarezii*** **(µg/kg fresh weight)**	**(µg/mL of extract)**
Auxin content	–	5500 [a,b,c]	–
Indole acetic acid (IAA)	–	–	3.87-160 [b,c,d,e,g]
Gibberellins content (GA_3, GA_7)	157 [a]	–	–
GA_3	–	–	23.65-128 [c,d,e]
GA_7	–	–	110 [d]
Cytokinins content (trans-zeatin, kinetin)	15.3 [a]	–	–
Cis-zeatin	–	–	20.10-117 [c,d,e,f,g]
Trans-zeatin	–	–	12.4 [b]
Kinetin	–	–	7.94-73 [c,d,f,g]
Choline	–	–	57.30 [e]
Glycine betaine	–	–	79.33 [e]

* Ranges of all values found in literature.
[a] (Hong et al., 2007); [b] (Das and Prasad, 2015); [c] (Prasad et al., 2010); [d] (Sedayu and Basmal, 2013); [e] (Layek et al., 2015); [f] (Zodape et al., 2009); [g] (Mondal et al., 2015).

benzylaminopurine (6-BA) and a reduction of the callus induction time with the addition of spermine has been reported (Muñoz et al., 2006). Additional studies demonstrated an increased growth rate, regeneration of explants, and shoot formation in micropropagules using spindle inhibitors such as colchicine and oryzalin alone or in combination with indole-3-acetic acid (IAA), 6-BA, spermine and kinetin (Hayashi et al., 2007; Neves et al., 2015) and the Acadian marine plant extract powder (Yunque et al., 2011; Tibubos et al., 2017).

The successful use of airlift bioreactors to produce seaweed biomass involving prior stimulation with phytohormones was reported by (Yong et al., 2014). In their *in vitro* study, an improved regeneration and growth of *K. alvarezii* propagules was observed using a dose-dependent application of 6-BA and IAA under control parameters such as pH, salinity, light, and culture intensity in Provasoli's enriched seawater media.

Another alternative to promote the production of seed stock for commercial cultivation of *Kappaphycus* species is using seaweed liquid fertilizers. Application of the commercially available extract of *Ascophyllum nodosum* containing plant hormone regulators, macro- and micronutrients in a dose-dependent manner improved the daily growth rate of *K. alvarezii* strains with reaching almost the double growth rate of the control and reduced the presence of epiphytes and the "ice-ice" disease (Loureiro et al., 2010). It was noticed that brown and green strains of *K. alvarezii* had better growth rates than the red strain. The use of Acadian marine plant extract alone or in combination with phytohormones to promote micropropagation of *K. alvarezii* microplantlets has been recommended (Hurtado et al., 2008).

Commercially cultivated microalgae are other organisms that showed significant improvement in their growth and higher yield of their bioproducts through the application of phytohormones from seaweeds. Microalgae represent an important and sustainable source for animal feed in aquaculture based on their high nutritional content and as a bioremediation tool to prevent eutrophication in a high-ammonia-nitrogen environment (Zhao et al., 2019; Nagarajan et al., 2021). Different concentrations of *K. alvarezii* sap were used as biostimulant to enhance the growth and biochemical composition of *Chlorella variabilis* (Sati et al., 2021). The lipid and carbohydrate concentration of the latter microalga were increased up to 50 and 100% when sap concentration was used at 0.6 and 1%, respectively. Even though, very little investigation has been carried out with *Kappaphycus* sap containing phytohormones, several studies demonstrated the potential use of plant growth regulators to improve biomass productivity and chemical composition of microalgae (Hunt et al., 2010; Babu et al., 2017; Touliabah and Almutairi, 2021), especially under stressful conditions (Sun et al., 2018; Zhao et al., 2019).

4.2.2 *Acanthophora* spp.

The phytohormone composition and content of *Acanthophora* species have not been evaluated in detail. To the best of our knowledge, there is currently only one scientific report of the phytohormone content of *A. spicifera*, namely of one collected in Vietnam (Table 4), and no publications on the phytohormone content of extracts of this species have been reported.

4.3 Pigments

Red seaweeds are known to produce a diverse group of pigments, such as (1) the phycobiliproteins Rhodophyta phycoerythrin (R-PE) (red color), Rhodophyta phycocyanin (R-PC) (blue color) and allophycocyanin (APC), (2) carotenoids, (3) xanthophylls and (4) chlorophyll *a* (Chl *a*) (Freitas et al., 2021). These compounds have an important role in seaweed growth and development by harvesting solar energy and transforming it into chemical energy. As a high-added value, these compounds have displayed important bioactivities in the pharmaceutical industry as antioxidant (β-carotene) and anticancer agents used in photodynamic therapy (Chl *a*), in the textile industry as natural dyes (carotenoids, Chl *a*) (Ab Kadir et al., 2014) and as human-safe food colorant (Heriyanto et al., 2015). In the aquaculture sector, pigments like lutein, astaxanthin, chlorophylls, phycobiliproteins and β-carotene are used to improve the color, health, and organoleptic properties of commercially important marine organisms (Serive and Bach, 2018). However, the cost of production of these pigments is very high and has been limited by production technologies (Yusoff et al., 2020). It is necessary to do more research on the development of more effective, low cost and sustainable pigment production to be used in aquaculture. Although, most of the pigments used for aquaculture are obtained from microalgae (Yusoff et al., 2020), it is important to search for other natural sources such as seaweeds, that could provide good quality and quantity of pigments and find their way as functional food in the aquaculture industry.

4.3.1 *Kappaphycus* spp.

Studies in *K. alvarezii* reported the presence of R-PE (Naguit and Tisera, 2009; Heriyanto et al., 2015; Banu et al., 2017; Deepika, 2018; Ganesan and Shanmugam, 2020; Uju et al., 2020), R-PC, Chl *a*, chlorophyllide *a*, pheophytin, α-cryptoxanthin, violaxanthin, antheraxanthin, zeaxanthin, β-carotene, α-carotene, trans-fucoxanthin and other unidentified pigments (Naguit and Tisera, 2009; Heriyanto et al., 2015; Brotosudarmo et al., 2018) (Table 5). Variation of their composition between strains, depths of cultivation and subjection to stress conditions such as UV radiation have also been documented (Eswaran et al., 2001; Schmidt et al., 2010).

Although, the application of pigments isolated from *Kappaphycus* spp., in aquaculture has not been reported, the application of *K. alvarezii* sap could be used during the cultivation of astaxanthin-rich organisms such as *Haematococcus pluvialis* or β-carotene-rich sources such as *Dunaliella salina* to enhance its yield (Xie et al., 2018). The use of carotenoids as food ingredients for aquaculture has been reviewed (Pereira da Costa and Campos, 2020). Studies on C-PC produced by cyanobacteria (*Spirulina platensis*) have shown to improve growth and color of the guppy fish *Poecilia reticulata* (Biabani Asrami et al., 2019), reduce cannibalism and enhance survival and disease resistance against *Vibrio alginolyticus* in the Asian seabass *Lates calcarifer* larvae (Gora et al., 2019) and induce a non-specific immune response in the fish carp *Cyprinus carpio* (Muchtar et al., 2019). R-PE isolated from the red alga *Colaconema* sp. induced an immunostimulatory effect on the shrimp *Litopenaeus vannamei* with increasing resistance against *Vibrio parahaemolyticus* and white spot syndrome virus (Lee et al., 2021). The strategies to improve yield and chemical stability of PE and PC have been recently reviewed (Hsieh-Lo et al., 2019).

TABLE 5 Pigment content in *Acanthophora* and *Kappaphycus* species.

Parameter *	*A. spicifera*	*A. nayadiformis*	*K. alvarezii*
Chl *a*	0.056 - 0.50 *a*,[o] ** 0.094 – 0.37 [b,c] ***	0.20 – 1.60 [f] **	0.012 – 2.7 g,[h,i,j,k,l,m,n] ***
APC	0.031 – 0.5 *a*,[c,d] ** 0.121 [e] ***	nd	nd
R-PC	0.057 – 0.9 *a*,[d] ** 0.24 – 0.34 [c,e] ***	1.68 – 6.04 [f] **	0.203 – 0.491 l,[m] ***
R-PE	0.143 – 2.6 *a*,[d] ** 0.42 – 0.49 [c,e] ***	2.20 – 10.03 [f] **	1.2 – 1.7 l, [m] ***
Zeaxanthin	nd	0.02 – 0.05 [f] **	0.0013 – 0.003 [i] ***
α-carotene	nd	nd	0.002 – 0.054 [i,n] ***
β-carotene	nd	0.02 – 0.08 [f] **	0.05 – 0.514 [i,n] ***
α-cryptoxanthin	nd	nd	0.005 – 0.037 [n] ***
Antheraxanthin	nd	nd	0.007 – 0.053 [n] ***
Lutein	nd	0.02 – 0.09 [f] **	nd
Total carotenoids	0.245 – 0.379 *a* ** 0.31 [b] ***	nd	nd

* Ranges of all values found in literature; nd= not determined
** values expressed as mg/g dry weight (dw)
*** values expressed as mg/g fresh weight (fw)
[a] (Pereira et al., 2017); [b] (Seenivasan et al., 2012); [c] (Arunkumar et al., 2014); [d] (Martins et al., 2018); [e] (Senthilkumar et al., 2013); [f] (Petrocelli and Felicini, 1995); [g] (Hong et al., 2007); [h] (Naguit and Tisera, 2009); [i] (Brotosudarmo et al., 2018); [j] (Paransa et al., 2020); [k] (Rajaram et al., 2021); [l] (Eswaran et al., 2001); [m] (Periyasamy et al., 2019); [n] (Heriyanto et al., 2015), [o] (Dawes et al., 1978).

Extraction optimization of pigments such as R-PE (Uju et al., 2020), β-carotene and chlorophyll (Baskararaj et al., 2019) and carrageenan (Mahyati and Azis, 2019) from *K. alvarezii* has been reported. (Freitas et al., 2021) provided an interesting review of the chemical diversity of the different pigments produced by red seaweeds and their biotechnological applications along with the number of patents registered.

4.3.2 *Acanthophora* spp.

Information on the pigment content in *Acanthophora* spp. is rather limited. *A. spicifera* contained 0.34 mg of R-PC, 0.121 mg of R-APC and 1.061 mg of R-PE per gram fresh weight (Senthilkumar et al., 2013; Pereira et al., 2019) while *A. nayadiformis* contained 0.20-0.28 mg/g dry weight of Chl *a*, 2.20-5.54 mg/g dry weight of R-PE and 1.68-3.91 mg/g dry weight of R-PC (Petrocelli and Felicini, 1995) (Table 5).

Concentrations of 0.79-2.39 mg/g dry weight of lutein, 5.79-11.28 mg/g dry weight of zeaxanthin, 1.59-16.16 mg/g dry weight of α-carotene were reported (Pereira et al., 2019), while antheraxanthin, β-cryptoxanthin and β-carotene were identified in *A. spicifera* based on their retention time and comparison with standards (Aihara and Yamamoto, 1968). Also, the concentration of 0.02 mg/g dry weight of β-carotene, 0.02 mg/g dry weight of zeaxanthin, and 0.02 mg/g dry weight of lutein were reported for *A. nayadiformis* (Petrocelli and Felicini, 1995).

4.4 Amino acids and peptides

Seaweed-derived peptides such as lectins and phycobiliproteins and the mycosporine-like amino acids (MAAs) have been studied for their wide diversity of applications in food, pharmaceutical and cosmeceutical sector (Lafarga et al., 2020; Vega et al., 2021; Echave et al., 2022). One of the most important seaweed peptides with aquaculture applications are lectins, of which the advances in the development of extraction methods and the wide range of biological activities was recently reviewed (Maliki et al., 2022). In this review, phycobiliproteins are being considered within the pigment section.

Lectins are glycoproteins of non-immune origin characterized for their high capacity and selectivity to reversibly bind to carbohydrate moieties present in pathogens through a carbohydrate recognition domain (Mishra et al., 2019). Seaweeds are known to be a good source of a vast diversity of novel bioactive lectins also called phycolectins. Red seaweed lectins are classified depending on their carbohydrate specificity in complex-type specific (complex N-glycan or complex O-glycan or both), high-mannose type specific or both complex and high-mannose glycan specific lectins (Singh and Walia, 2018). The gamete recognition during sexual reproduction is suggested to be one of the most important roles of lectins in marine algae.

The MAAs are low molecular weight and nitrogen-containing compounds with strong photoprotective activity against ultraviolet radiation (Oren and Gunde-Cimerman, 2007). These UV-absorbing compounds are found in many marine organisms like cyanobacteria, cnidarians, fungi, but are in greater content present in red seaweeds (Bedoux et al., 2020). The distribution, concentration, and types of MAAs in seaweeds and the development of an open database for these metabolites have been reported (Sun et al., 2020). These secondary metabolites play an important role in the photosynthesis as light-harvesting pigments, provide protection to the organism against desiccation or thermal stress, as antioxidants, with anti-lipid oxidation activity, and as intracellular nitrogen reservoir. These molecules are widely used in the cosmeceutical industry based on their antioxidant, anti-inflammatory, and collagen, elastin and DNA protective activities, and their distribution in seaweeds has been reviewed (Vega et al., 2021). Although, there is little application of MAAs in aquaculture, their presence in seaweeds and other aquatic animals provides them protection against solar radiation conditions and accumulation of these important metabolites in seaweeds would provide an economic alternative to be exploited for the cosmeceutical industry.

4.4.1 *Kappaphycus* spp.

Kappaphycus species are a rich source of essential amino acids required for human and animal consumption.

The presence of lectins has been reported in *K. alvarezii* (Hung et al., 2009b; Hung et al., 2009c; Sato and Hori, 2011; Yong et al., 2014) and *K. striatus* (Hung et al., 2009b; Hung et al., 2009c; Hung et al., 2019; Hung and Trinh, 2021). They have been shown to be highly specific for high-mannose N-glycans and have displayed potential biological activities as antiviral and anticancer agents and possess strong divalent cation-independent hemagglutination activity (Hung et al., 2009b; Sato and Hori, 2011; Hirayama et al., 2016; Hung and Trinh, 2021). Other studies reported that the three color morphotypes of *K. alvarezii* red, brown, and green strains, also contain similar lectin content, however, the lectin yield of the red strain was higher than the green and brown strains (Hung et al., 2009a). It has been suggested that lectin biosynthesis in macroalgae is enhanced by an increased uptake of inorganic nitrogen in ammonium (NH_4^+) form rather than nitrate (NO_3^-), especially during low seawater temperature, solar radiation, and low tide (Hung et al., 2009b). Whereas the application of seaweed-derived mannose-specific lectins has been focused mostly on the pharmacological potential for humans (Barre et al., 2019), very little research has been undertaken in the application of

Kappaphycus-derived lectins in aquaculture. The only study reported by (Hung et al., 2015), revealed inhibition of the growth of the shrimp pathogens *Enterobacter cloacae* and *Vibrio alginolyticus* by the isolated lectin KSA-2 from *K. striatus*. Even though this lectin did not show growth inhibition against *V. parahaemolyticus* and *V. harveyi* in the same study, it has great potential to target aquaculture pathogens with glycoproteins with high-mannose N-glycans in their surface.

To the best of our knowledge, to date, there are no studies determining the MAAs composition and their concentration in *Kappaphycus* species.

4.4.2 *Acanthophora* spp.

Seaweeds are becoming an important source of high-nutritional and low-cost material for the development of animal feed. Analysis of the amino acid and peptides content of *A. spicifera* (Wahidulla et al., 1991; Lourenço et al., 2002; Vinoj Kumar and Kaladharan, 2007; Dixit et al., 2018), *A. muscoides* (Rao, 1970) and *A. nayadiformis* (Lewis and Gonzalves, 1962; Impellizzeri et al., 1975) have been reported. *Acanthophora* species are not a very good source of essential amino acids, as the estimated protein content is only in the range of 5-25% of its dry weight. Protein is one of the most important and expensive ingredients in feed for aquatic animals. The quality of a protein in feed depends mainly on its amino acid profile and digestibility. Therefore, the analysis of the amino acid profile is necessary for the elaboration of animal diets, in accordance with the amino acid's requirements of the animal of interest.

The presence of lectins in *A. spicifera* was first deducted by the strong agglutinin activity of rabbit erythrocytes (Chiles and Bird, 1989) and the enzyme treated erythrocytes from chicken, rabbit, goat, pig, and human O type (Lima Ainouz et al., 1992; Mangaiyarkarasi et al., 2014) and from *A. muscoides* (Anam et al., 2019). However, there are no studies on the application of *Acanthophora* lectins in aquaculture.

The MAAs, such as asterina-330, gadusol, mycosporine-glycine, mycosporine-2-glycine, mycosporine-taurine, mycosporine-methylamine-serine, mycosporine-methylamine-threonine, palythinol, palythene, palythine, palythine-serine, palythine-serine-sulfate, palythine-threonine, porphyra-334, shinorine, and an unknown compound with maximum absorption at 299 nm have only been reported for *A. spicifera* (Karsten et al., 1998; Rosic et al., 2015; Muthiah et al., 2017). Although the UV-absorbing compounds asterina-330, mycosporine-glutamic acid and palythinol have been suggested to be present in *A. muscoides* (Tanaka et al., 2020), further studies are required to confirm their presence and concentration in this and other species of *Acanthophora*.

An increased metabolic rate and faster hatching egg hatchering were observed in the sea hare *Aplysia dactylomela* after feeding with *A. spicifera* as a rich source of MAAs (Carefoot et al., 1998). Further studies suggested the role of MAAs as UV protectant in *A. dactylomela* as these metabolites were distributed in the skin (Carefoot et al., 2000) and the fish *Thalassoma duperrey* after feeding with *A. spicifera* (Zamzow, 2004). The increase in MAAs content in the fish mucus was only observed when exposed to UV radiation, and accumulation of MAAs was higher in male fish than female. The UV photo-protective effect on other marine organisms such as the sea urchin *Strongylocentrotus droebachiensis* (Adams and Shick, 1996), and different species of holothuroids (Shick et al., 1992) has been reported. The presence of UV-absorbing compounds in the sea hare and fishes is resulting from their diet with seaweeds rich in MAAs. The chemical and ecological role of MAAs and their distribution among marine organisms have been reviewed (Carreto and Carignan, 2011).

Despite the few studies on the role of MAAs from *Acanthophora* species in aquaculture, these metabolites play a very important role in the protection of animals against radiation. The protective role of MAAs in aquatic animals has been reported in different animals. For example, studies on the sea hare *Aplysia californica* indicated the presence of MAAs and their role as a mechanism of chemical defense or as intraspecific alarm cues. Two undescribed MAAs such as aplysia palythine A and aplysia palythine B and the known asterina-330 were found in the sea hare after feeding with the red algae *Gracilaria ferox* and *Agardhiella subulate* (Kicklighter et al., 2011).

MAAs can be transferred from different trophic levels, and might play different roles in the marine environment, especially increasing the survival of species under high UV radiation and predation environments. Solar radiation causes damage to the marine environment and its fauna by reducing productivity, growth rate and development, and the mutation rate in eggs and larval stages of marine animals and algae is increased (Häder et al., 2007). Feeding commercially important species of marine animals with seaweeds rich in MAAs in tropical zones with higher exposure to solar radiation could enhance their survival, growth rate and reproduction with reduced economic impact. Additionally, when culturing seaweeds in high nitrogen environments, the concentration of MAAs in seaweeds would increase, as reported by a previous study on *Gracilaria tenuistipitata* (Barufi et al., 2012).

5 Discussion and research gaps

Further valorization of *Kappaphycus* spp. and *Acanthophora* spp. in the aquaculture sector will need to bridge the following research gaps:

(1) For at least one of the studied species the proof-of-principle of certain innovative applications of seaweed biomass, extracts and biochemicals in the aquaculture sector has been shown. These applications remain to be

confirmed for the other species as well to open commercial opportunities for the seaweed biomass and their bioproducts.

(2) Similarly, other innovative aquaculture applications have been demonstrated for other seaweed species and their chemical arsenal. This suggests that some opportunities are available to explore these applications for *Kappaphycus* spp. and *Acanthophora* spp. by means of scientific research.

(3) Another remaining challenge is to standardize the methods to analyze the chemical profile and to quantify their concentration/content. Furthermore, concerted efforts are needed towards the standardization of the methodology to report data. This will allow a more accurate comparison of different studies, especially with respect to units (reporting of the content of chemical compound per fresh weight seaweed, dry weight seaweed, and volume of extract).

(4) To discover new biochemical compounds and identify new applications of these compounds, an in-depth chemical profiling of *Kappaphycus* spp. and *Acanthophora* spp. in different geographical locations and temporal variations needs to be carried out.

The available information highlights the great potential application of both genera of red seaweeds in aquaculture that will allow researchers to further develop the production of innovative seaweed-based bioproducts.

Local tropical seaweed species are yet to be fully utilized, especially as a primary product to be used in the development of natural bioproducts to achieve a more resilient aquaculture and agriculture. Therefore, more attention should be given to underutilized local tropical seaweed species.

6 Conclusions

The chemical diversity (polysaccharides, phytohormones, pigments, amino acids and peptides) of *Kappaphycus* and *Acanthophora* has shown promising applications for aquaculture, including pathogen control, immunostimulant, antioxidant, bioremediation, feed, UV protectants, increase in seafood shelf life, animal colorant, and growth regulator for microalgae culture. This review justifies further research of the latter species to guarantee seaweed biomass availability, to know the temporal and spatial variation of the chemical composition of seaweeds, to standardize research methodologies, and to confirm the bioactivity of phytochemicals, amongst others. This study contributes to boosting the applications of these and other red seaweeds in the aquaculture sector and, by this, helping stakeholders to benefit from these seaweeds by diversifying the blue bioeconomy in tropical countries. The authors would like to thank the reviewers for their valuable comments to improve the manuscript.

Author contributions

PG, PM, SM, OC, PB and SH contributed to the initial idea and design of the manuscript. PG collected the literature and wrote the original draft of the manuscript. PM contributed to table data collection and reference listing. SH did literature survey, contributed to writing the abstract, research gaps, conclusions, and edited the total manuscript. SM revised the manuscript. All authors contributed to the article and approved the submitted version.

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Conflict of interest

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

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