


Review

Distribution, Contents, and Types of Mycosporine-Like Amino Acids (MAAs) in Marine Macroalgae and a Database for MAAs Based on These Characteristics

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Received: 27 November 2019; Accepted: 1 January 2020; Published: 7 January 2020



Abstract: Mycosporine-like amino acids (MAAs), maximally absorbed in the wavelength region of 310–360 nm, are widely distributed in algae, phytoplankton and microorganisms, as a class of possible multi-functional compounds. In this work, based on the Web of Science, Springer, Google Scholar, and China national knowledge infrastructure (CNKI), we have summarized and analyzed the studies related to MAAs in marine macroalgae over the past 30 years (1990–2019), mainly focused on MAAs distribution, contents, and types. It was confirmed that 572 species marine macroalgae contained MAAs, namely in 45 species of Chlorophytes, 41 species of Phaeophytes, and 486 species of Rhodophytes, and they respectively belonged to 28 orders. On this basis, we established an open online database to quickly retrieve MAAs in 501 species of marine macroalgae. Furthermore, research concerning MAAs in marine macroalgae were analyzed using CiteSpace. It could easily be seen that the preparation and purification of MAAs in marine macroalgae have not been intensively studied during the past 10 years, and therefore it is necessary to strengthen the research in the preparation and purification of MAA purified standards from marine macroalgae in the future. We agreed that this process is not only interesting, but important due to the potential use of MAAs as food and cosmetics, as well as within the medicine industry.

Keywords: CiteSpace analysis; marine macroalgae; mycosporine-like amino acids; online database for MAAs; photoproduction

1. Introduction

MAAs (mycosporine-like amino acids) are natural compounds with low molecular weight and exist in diverse aquatic organisms, from algae [1–7] to phytoplankton [2,7–12], cyanobacteria [2,7,13–15], microorganisms [16,17], and marine animals [18–21].

MAAs have maxima absorption ranging between 310 and 360 nm [22]. They constitute a class of more than 30 related UV-absorbing compounds with molecules constituted by imino-carbonyl derivatives of mycosporine cyclohexenone chromophore [7,23]. MAAs exhibited the scavenging effects of oxygen free radicals [24,25], anti-lipid oxidation activity [26], a regulatory role in plant growth

and development [27], and so on [28]. Meanwhile, MAAs may also possess many physiological functions, including the protection of antitumor activity [29], embryonic and larval development [30], reproduction regulation [23], and osmotic regulation [31].

MAAs were found in marine organisms in the 1960s [17]. However, research pertaining to MAAs in marine macroalgae gradually attracted the attention of researchers in the 1990s [32–34]. More exactly, most studies concerning MAAs in marine macroalgae focused on the period of 1998–2009 [2,4,5,7,35,36]. During this period, MAAs in more than 300 species of marine macroalgae were determined, for example, the green algae *Acrosiphonia arcta* [4], *Boodlea composite* [5], *Prasiola crispa* ssp. *antarctica* [3], *Prasiola crispa* [35] and others macroalgae [4,5,7] in Chlorophyta; a class of the brown algae in Phaeophyta, *Ecklonia radiata* [37], *Halopteris scoparia* [4], *Hydroclathrus clathratus* [5], *Laminaria saccharina* [38], and others brown algae [4,5,7]; many red algae of Rhodophyta, *Ahnfeltiopsis devoniensis* [39], *Apophlaea lyallii* [37], *Bangia atropurpurea* [40], *Chondrus crispus* [41], *Gracilaria chilensis* [42], *Iridaea* sp. [43], *Palmaria palmata* [44], *Porphyra umbilicalis* [1] and etc. [4,5,7,45,46]. From 2009 to 2019, MAAs in less than 200 species, such as *Bangia atropurpurea* [47], *Calliarthron tuberculosum* [48], *Catenella repens* [49], *Gelidium lingulatum* [50], *Gloiopeltis furcate* [51], *Palmaria palmata* [52], *Pyropia plicata* [53], *Solieria chordalis* [54] and others macroalgae [55–58], were found.

Marine macroalgae as marine primary productivity have developed complex and unique metabolic pathways. Therefore, they have been become the target of exploiting natural bioactive components. To date, MAAs in more than 500 marine macroalgae have been reported. However, unfortunately, the summary and generalization about these researches were lacked. This made it very difficult to provide relevant information on MAAs of marine macroalgae. Therefore, this paper will provide an overview of MAAs in marine macroalgae since 1990 and focus on the contents and types of MAAs, and their distribution in marine macroalgae. The two databases related MAAs in marine macroalgae have been showed [2,59]. Although these two databases were not specific databases for MAAs in marine macroalgae, and provide less information regarding MAAs, the lack of total MAAs contents and specific MAA content, these works provided us with a good idea. Therefore, further in paper we established an open online database for MAAs in 501 species of marine macroalgae to quickly retrieve some related information regarding MAAs in marine microalgae since 1990. A lot of information, such as the source (field/culture) and collection site of marine macroalgae, the total MAAs contents, specific MAA content, and/or MAAs composition etc., were included in this online database (<http://210.28.32.218/MAAs/>).

CiteSpace was a software used in scientific literature to identify and display new trends of scientific development [60]. Finally, in this review, the development tendency of the studies about MAAs in marine macroalgae will be analyzed using CiteSpace to point out future research directions for researchers in related fields. This is not only very interesting, but also can promote the development of MAAs in marine macroalgae.

2. Results

2.1. MAAs Distribution, Contents and Types in Marine Macroalgae

In our survey that summarized of more than 660 species, 572 species of marine macroalgae contained MAAs, found namely in 45 species in Chlorophyta, 41 species in Phaeophyta, and 486 species in Rhodophyta (Figure 1), and they respectively belonged to 28 orders (Figure 2). Among them, marine macroalgae which contained MAAs mainly distributed in orders Bangiales, Ceramiales, Gigartinales, and Gracilariales. MAAs represent a class of the secondary metabolites in marine macroalgae [61,62], and in addition to antioxidant [24–28] and anti-ultraviolet radiation activities [22,23,63], likely possess many physiological activities, such as capacity to inhibit the proliferation of tumor cells [29], protecting embryonic and larval development [30], and regulating reproduction [23] and osmosis [31].

The research efforts made pertaining to MAAs in marine macroalgae have drawn significant attention since 1990. The contents and composition of MAAs in marine macroalgae were important

in developing MAAs. Therefore, the summary and analysis of total MAAs contents and MAAs composition in marine macroalgae have been conducted according to different orders in this paper (Figures 2–4).

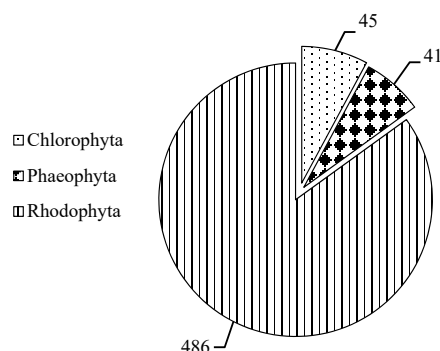


Figure 1. Distribution of MAAs in different phyla of marine macroalgae. Data extracted from related studies since 1990, and the number in a pie chart represents the total number of marine macroalgae species belong to this phylum.

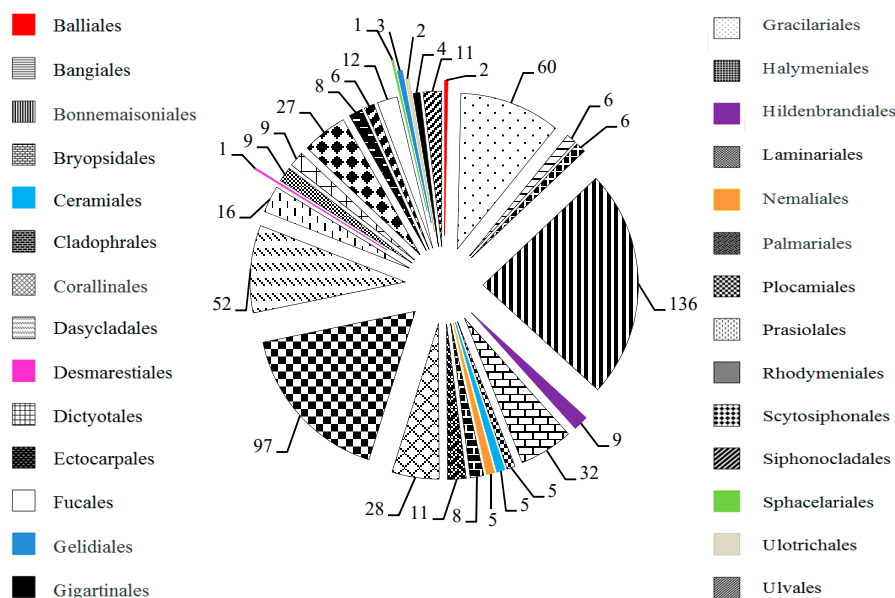


Figure 2. Distribution of MAAs in different orders of marine macroalgae. Data extracted from related studies since 1990, and the number in a pie chart represents the total number of marine macroalgae species belong to this order. The several highlights parts in the pie chart are just for clarity.

MAAs have been found in 45 species of the green algae in Chlorophyta [2–5,7,35,64]. Among them, total MAAs contents were determined in only 12 species. The green algae with high total MAAs contents belong to Prasiolales, and contents were more than 3.5 mg/g DW (Figure 3a), such as *Prasiola crispa* ssp. *antarctica* [3], *Prasiola crispa* collected from South Shetlands [40] and Kongsfjorden [35] respectively. The total MAAs contents in other macroalgal Chlorophytes were very low, with values ranging between 0.0045 and 0.275 mg/g DW. Therefore, some bars which represent the total MAAs contents in different marine Chlorophytes were almost on the ordinate.

The brown algae (41 species) in Phaeophyta also were confirmed to contain MAAs [2–5,32,37,38] (Table 1). Further, for eight species, namely *Chorda tomentosa* [4], *Desmarestia menziesii* [32], *Dictyota bartayresii* [5], *Dictyosiphon foeniculaceus* [4], *Pilayella littoralis* [4], *Ecklonia radiata* [37], *Halopteris scoparia* [4], *Hydroclathrus clathratus* [5] and *Sargassum oligocystum* [5], the total MAAs contents were pointed out. These values were very low and less than 0.2 mg/g DW (Figure 3b).

A total of 486 MAA-containing strains of macroalgal Rhodophytes were detected. In order to present these reports from 1990 to 2019 more clearly, they are shown in two maps in Figure 3c,d, with 2009 as the cut-off time point. Among them, the total MAAs contents in 323 red algae were determined, and their MAAs contents were usually higher compared with macroalgal Chlorophytes and Phaeophytes [2–5,40,65]. For example, some members of orders Bangiales [5,40,65], Gracilariales [3,32,66], Gigartinales [5,40,42], and Gelidiales [48,67], their total MAAs contents ranges from 2 mg/g DW to nearly 20 mg/g DW. Of course, there were also many macroalgal Rhodophytes with lower total MAAs contents, such as *Actinotrichia fragilis* [5], *Asparagopsis taxiformis* [5], *Galaxaura oblongata* [5], *Gelidium corneum* [68], and *Georgiella confluens* [3], etc. [3–5,69], and these values were even less than 0.1 mg/g DW. Further, we classified these red algae into three groups according to their total MAAs contents. The first group, including 65 species belong to order Balliales, Ceramiales, Corallinales, Nemaliales and Rhodymeniales, exhibited low total MAAs contents (< 1 mg/g DW). A second group with the higher concentration of total MAAs and 52 species showed 1~2 mg/g DW MAAs. The last group that included 216 species, such as the orders Bangiales, Gelidiales, Gigartinales, and Gracilariales macroalgae showed the highest total MAAs contents and these values are all above 2 mg/g DW. Of note, *Rhodymenia* spp. Belonging to order Rhodymeniales had a surprisingly high MAAs contents (8.8–142.9 mg/g DW, average value 75.85 mg/g DW) [37]. This is clearly displayed in Figure 2c with another axe (maximum value of abscissa 80). In addition, the MAAs content value in each marine macroalgae could be obtained using the database (<http://210.28.32.218/MAAs/>) built by our team, which we will explain in detail later.

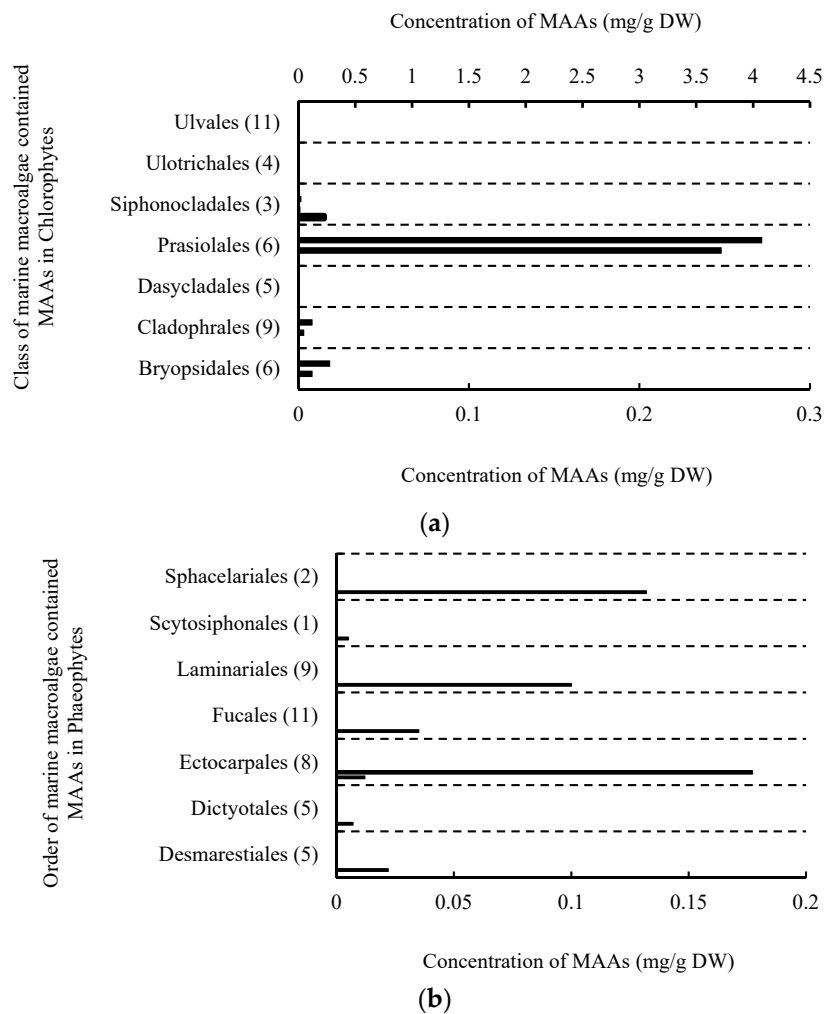


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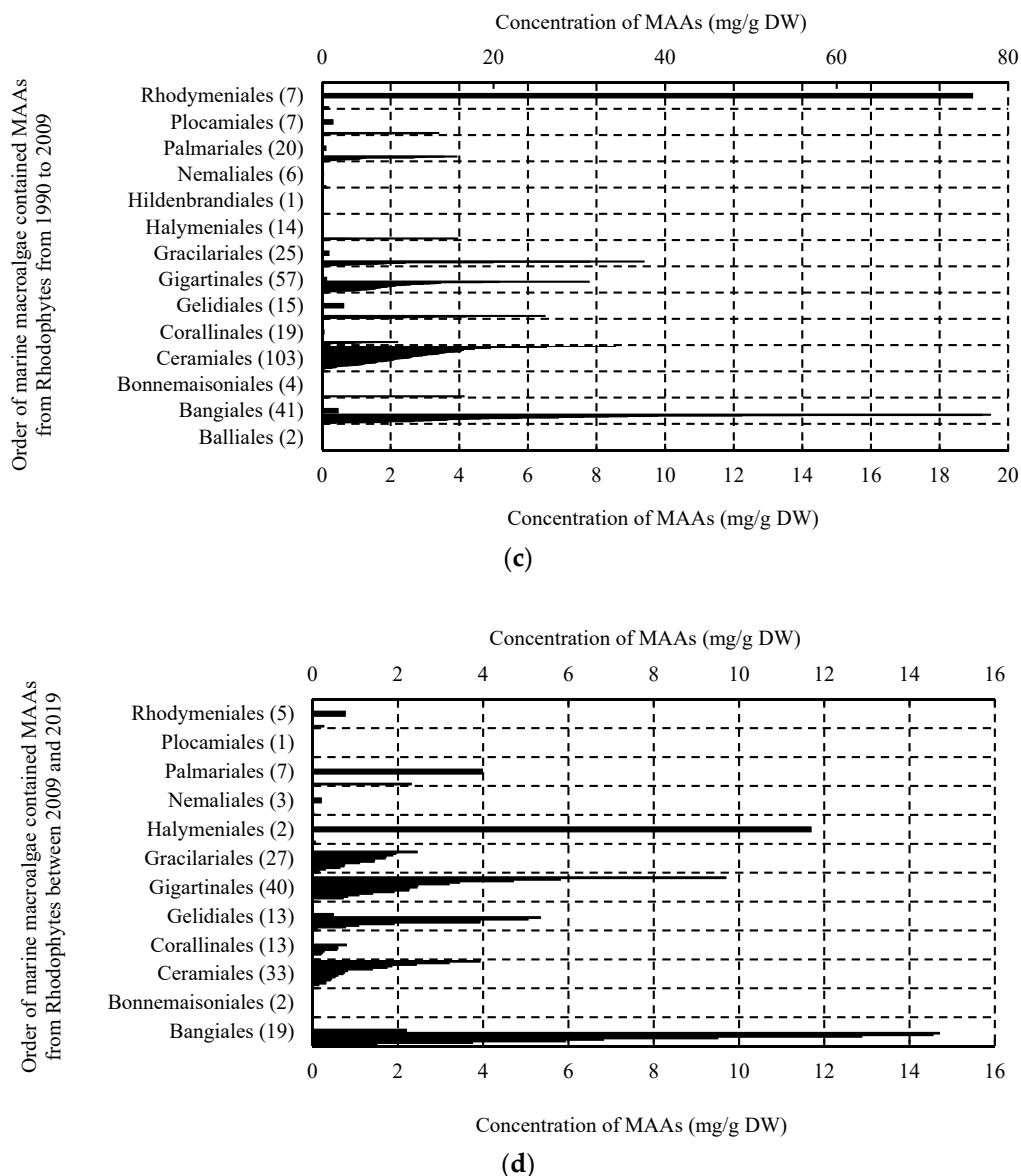


Figure 3. The contents of total MAAs in different orders of marine macroalgae. Data extracted from related studies since 1990. The number in bracket represents the number of species included in orders, bar represents a marine macroalgae with corresponding MAAs in (a–d), and the bars with different widths represent the numbers of some marine macroalgae with corresponding MAAs in (c,d).

From 1990 to 2019, the survey found that MAAs in marine macroalgae mainly focus on macroalgal Rhodophytes (Figure 1), therefore, MAAs types in Rhodophytes have been pointed out according to different orders of macroalgal Rhodophytes in this review (Figure 4). Identified MAAs in macroalgal Rhodophytes included 22 types, namely Aplysiapalythine A, Aplysiapalythine B, asterina-330, catenelline, mycosporine-alanine-glycine, mycosporine-glycine, mycosporine-methylamine-threonine, mycosporine-2-glycine, palythene, palythenic acid, palythanol, porphyra-334, palythine, shinorine, usujirene, and new MAAs prasiolin [70] and bostrychines A–F [71]. Among them, shinorine, porphyra-334, palythine and asterina-330 were more abundant, followed by palythanol; catenelline, mycosporine-2-glycine, mycosporine-methylamine-threonine and palythenic acid were very few. Among them, aplysiapalythine A, aplysiapaly thine B, catenelline, and novel MAAs (prasiolin and bostrychines A–F) were only found in macroalgal Rhodophytes [49,70–72]. Moreover, it is noted that MAAs have not yet been identified in many species of macroalgal Rhodophytes, and therefore it is quite possible that new MAAs will be discovered from those macroalgae. Seven MAAs, such as asterina-330,

mycosporine-glycine, palythene, palythinol, porphyra-334, palythine, and shinorine were found in macroalgal Chlorophytes and Phaeophytes, however other types MAAs have not been found in them except for unidentified MAAs. These results can be queried through the database mentioned above.

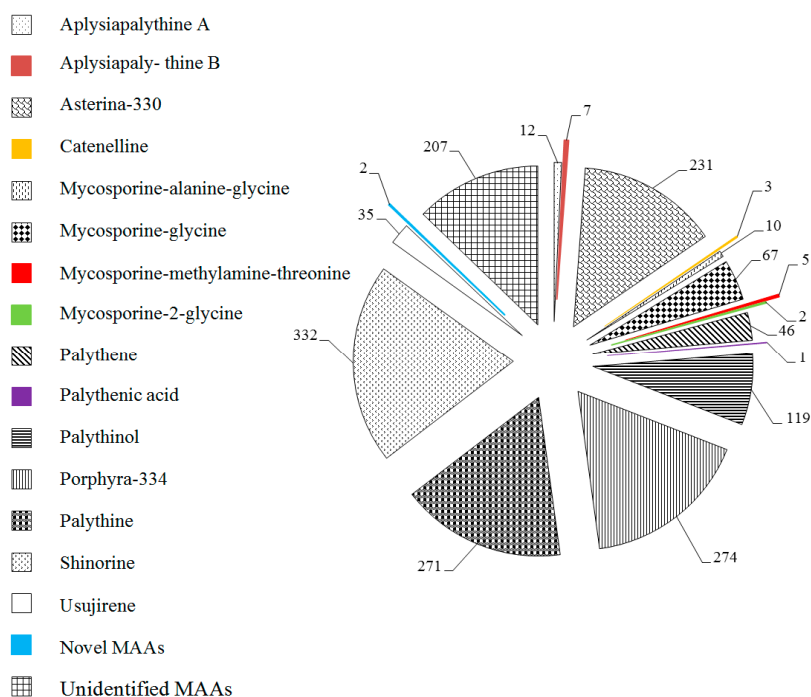


Figure 4. Types of MAAs in macroalgal Rhodophytes. Data extracted from related studies since 1990, and the number in a pie chart represents the total number of macroalgal Rhodophyta contained identical MAA. The several highlights parts in the pie chart are just for clarity.

In Figure 5, main MAAs in macroalgal Rhodophytes, such as asterina-330, mycosporine-glycine, palythene, palythinol, porphyra-334, palythine, shinorine and usujirene, were listed according to different orders. It can be clearly shown that these MAAs were common in marine macroalgae belonging to orders Ceramiales and Gigartinales macroalgae. Further, porphyra-334, palythine and shinorine were commonly found in orders Bangiales and Gracilariales macroalgae. And porphyra-334 and shinorine were also the most common in macroalgal Chlorophytes and Phaeophytes, but they usually occurred in lower concentrations. Meanwhile, mycosporine-glycine seemed to have the highest concentration in Chlorophytes and Phaeophytes species [4,5,73], for example, the proportion of mycosporine-glycine in MAAs for Chlorophytes *Boodlea composita* [5], *Chaetomorpha aerea* [4], *Codium fragile* [73], *Enteromorpha intestinalis* [73], *Halimeda polentia* [73], *Rhizoclonium tortuosum* [73], *Spongomorpha spinescens* [73], and *Ulva lactuca* [73] is more than 53%; in Phaeophytes *Agarum cribosum* [73], *Alaria esculenta* [73], *Ascophyllum nodosum* [73], *Chorda filum* [73], *Drsmarestia aculeata* [73], *Elachista fucicola* [73], *Fucus vesiculosus* [73], *Laminaria saccharina* [73], *Laminariocolas tomentosoides* [73], and *Sargassum fluitans* [73], this proportion was higher than 87%, even as high as 100% in *Alaria esculenta* [73], *Elachista fucicola* [73], *Fucus vesiculosus* [73], *Laminaria saccharina* [73], and *Laminariocolas tomentosoides* [73]. In Rhodophytes, such as *Acanthophora specifera* [5], *Chondrus crispus* [73], *Corallina officinalis* [73], *Cystoclonium purpureum* [73], *Lomentaria orcadensis* [73], *Mastocarpus stellata* [73], *Phycodrys rubens* [73], *Porphyra umbilicalis* [73], and other red algae [2–7,32–35,40,42–45,55,69,71,74–78], the proportion of mycosporine-glycine in MAAs was lower than 50%; and relatively numerous species (more than 260 species) did not detect this MAA, for instance, *Actinotrichia fragilis* [5], *Ahnfeltiopsis devoniensis* [39], *Amphiroa rigida* [2], *Asparagopsis armata* [4], and *Bangia atropurpurea* [3], etc. [1–5,40–42,44,55,58,65,67–72,74,76,79–87]. However, in Rhodophytes *Apophlaea lyallii* [37] and *Palmaria palmata* [73], the proportion of mycosporine-glycine in MAAs was very high. Therefore, those Chlorophytes [4,5,73], Phaeophytes [73],

and two Rhodophytes [37,73] species mentioned above were good sources of mycosporine-glycine. Some reports have determined that mycosporine-glycine, porphyra-334, and shinorine have better antioxidants properties [29,39,88,89], and therefore many macroalgal Rhodophytes species which belonged to the orders Bangiales, Ceramiales, Gigartinales, and Gracilariales have been considered to constitute prolific sources of porphyra-334 and shinorine, e.g., *Acanthophora specifera* [5], *Bangia atropurpurea* [65], *Caloglossa apomeiotica* [5], *Porphyra dioica* [57], *Bostrychia radicans* [40], *Ceramium nodulosum* [4], *Catenella impudica* [40], *Curdiea racovitzae* [32], *Gracilaria domingensis* [90], *Gymnogongrus griffithsiae* [4], and *Mastocarpus stellatus* [4], etc. [3,5,32,40,48,50,74,85,91–93].

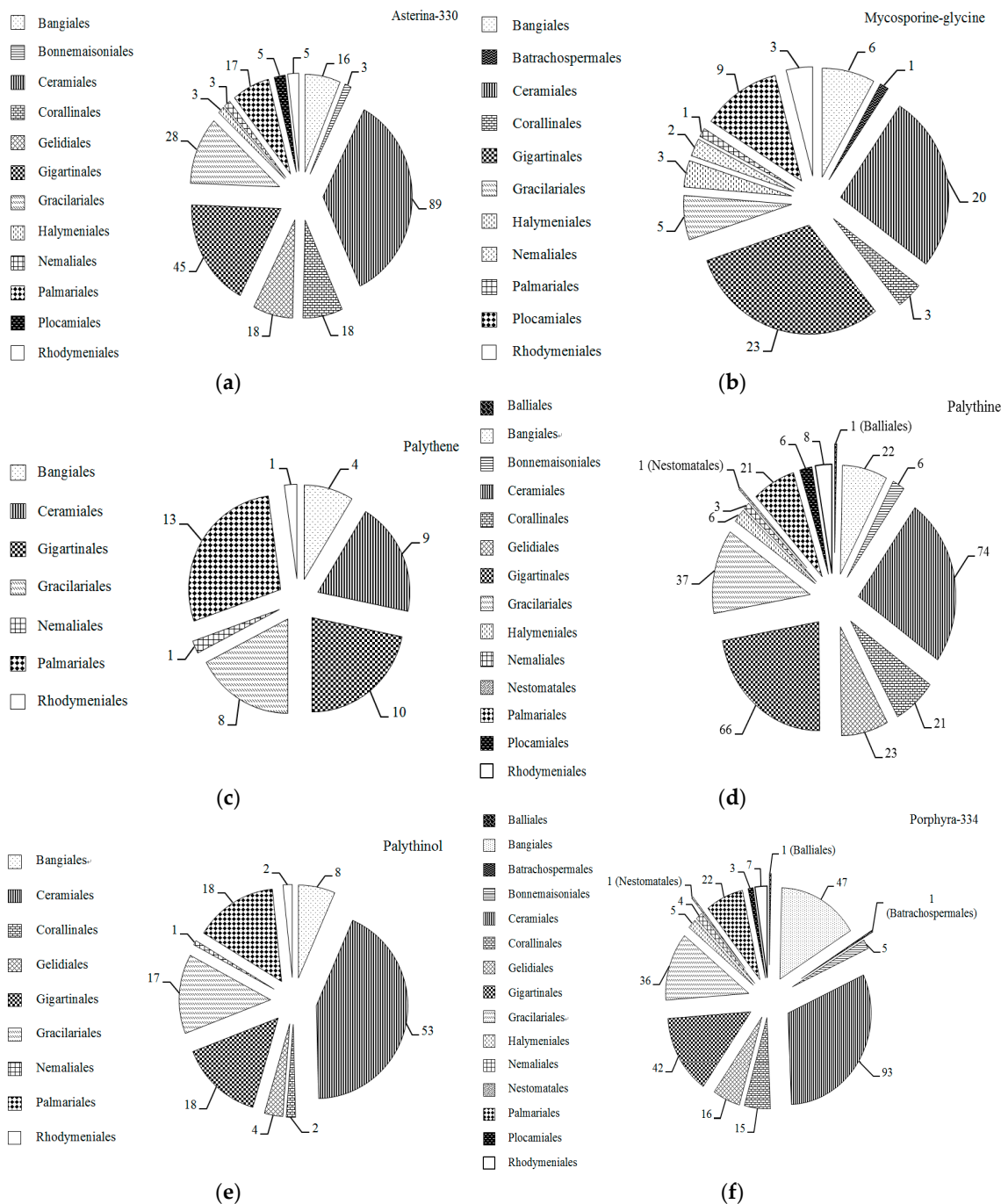


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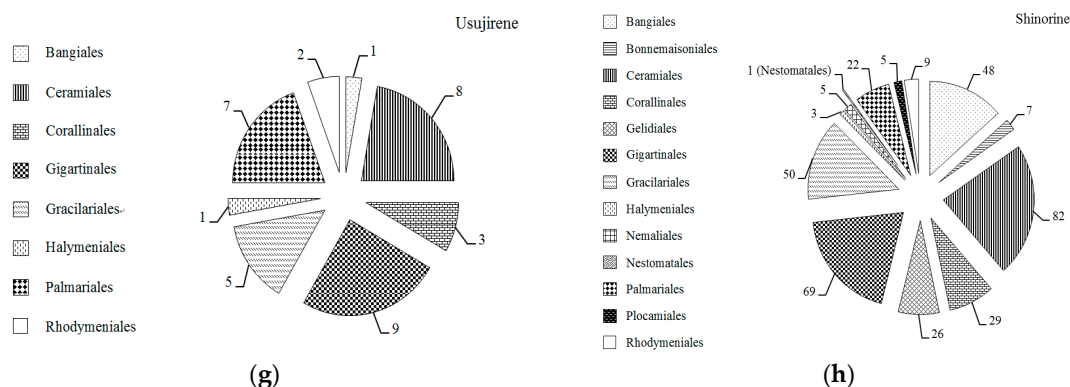


Figure 5. Distribution of specific MAA in different orders of macroalgal Rhodophytaes. Data extracted from related studies since 1990, and the number in a pie chart represents the total number of red macroalgae that contained specific MAA belong to this order. (a–h) represent specific MAA Asterina-330, Mycosporine-glycine, Palythene, Palythine, Palythinol, Porphyra-334, Usujirene and Shinorine, respectively.

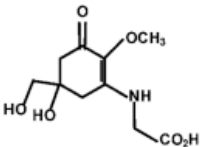
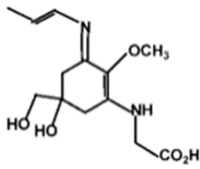
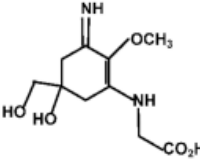
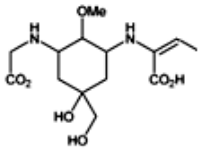
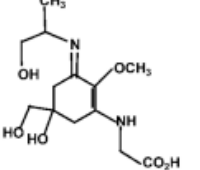
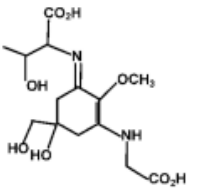
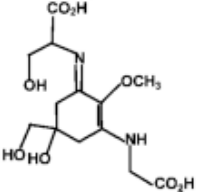
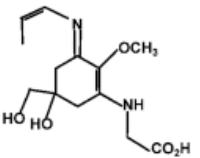
In addition, it is worth mentioning that the difference of the total MAAs or MAA value between cultivated marine macroalgae and field material existed from same collection location. For example, cultured *Stictosiphonia tangatensi* [40] exhibited only 47.8% of the total MAAs found in the field sample [5]. *Chondrus crispus*, which in culture exposed to green or blue light radiation, exhibited asterina-330, palythene, palythinol and shinorine that were lack of MAAs in the field sample. Similar phenomena also occurred in other seaweeds, such as *Bostrychia radicans* [5,40], *Caloglossa stipitata* [5,49], *Chondrus crispus* [60,72], *Kallymenia antarctica* [3], *Mazzaella laminarioides* [74], *Neuroglossum ligulatum* [3], *Palmaria decipiens* [3], *Plocamium cartilagineum* [3], *Porphyra columbina* [6,43], and *Porphyra endiviifolium* [3]. In the database that we set up later, we made clear the source of marine macroalgae that was field or culture, or commercial provision.

The specific parameters of 10 types of MAAs in marine macroalgae, such as structure, extinction coefficient, retention time and maximum absorption wavelength, have been showed in Table 1. Unfortunately, some parameters of these MAAs have not been determined, for instance, the extinction coefficient of mycosporine-2-glycine and usujirene. This should be due to the lack of commercially available MAAs standards.

Table 1. Structure, molar extinction coefficient, retention time, and maximum absorption wavelength of MAAs in marine macroalgae [43,94].

MAA	Structure	Extinction Coefficient ϵ ($M^{-1} cm^{-1}$)	Maximum Absorption Wavelength (nm)
Asterina-330		43800	330
Mycosporine-2-glycine		—	334

Table 1. Cont.

Mycosporine-glycine		28100	310
Palythene		50000	360
Palythine		35500~36200	320
Palythenic acid		29200	337
Palythanol		43500	332
Porphyra-334		42300	334
Shinorine		43700	334
Usujirene		—	357

In order to clearly present the distribution of specific MAA in each marine macroalgae, based on the literature information from the Web of Science, Springer, Google Scholar, and CNKI, Tables 2 and 3 are presented. In these two tables, all marine macroalgae were grouped according to the types of MAAs that they contained.

Table 2. MAAs in macroalgal Chlorophytes and Phaeophytes.

MAAs	Green Macroalgae	Ref.	Brown Macroalgae	Ref.
AS	<i>Codium adhaerens</i> , <i>Codium fragile</i>	[7]	<i>Padina crassa</i>	[5]
MG	<i>Boodlea composite</i> , <i>Chaetomorpha tortuosa</i> , <i>Codium adhaerens</i> , <i>Prasiola crassa</i> ssp. antarctica	[4,7,34]	<i>Desmarestia menziesii</i>	[5]
PE	<i>Caulerpa weberiana</i> , <i>Chaetomorpha tortuosa</i>	[7,34]		
PL	<i>Codium adhaerens</i>	[7]	<i>Padina crassa</i>	[5]
PR	<i>Acetabularia mediterranea</i> , <i>Acrosiphonia arcta</i> , <i>Acrosiphonia penicilliformis</i> , <i>Caulerpa racemosa</i> , <i>Cladophora rupestris</i> , <i>Codium adhaerens</i> , <i>Codium fragile</i> , <i>Dictyosphaeria cavernosa</i> , <i>Enteromorpha bulbosa</i> , <i>Ulva lactuca</i>	[2,4,5,7,75]	<i>Ascophyllum nodosum</i> , <i>Chorda tomentosa</i> , <i>Desmarestia aculeata</i> , <i>Desmarestia menziesii</i> , <i>Dictyosiphon foeniculaceus</i> , <i>Dictyota bartayresii</i> , <i>Halopteris scoparia</i> , <i>Himantothallus grandifolius</i> , <i>Hydroclathrus clathratus</i> , <i>Padina crassa</i> , <i>Pilayella littoralis</i> , <i>Sargassum oligocystum</i>	[3–5,7,34,75]
PI	<i>Acetabularia mediterranea</i> , <i>Cladophora rupestris</i> , <i>Codium adhaerens</i> , <i>Codium fragile</i>	[7,75]	<i>Desmarestia menziesii</i> , <i>Halopteris scoparia</i> , <i>Himantothallus grandifolius</i> , <i>Padina crassa</i> , <i>Sargassum oligocystum</i>	[3–5,7,48]
SH	<i>Acetabularia mediterranea</i> , <i>Caulerpa weberiana</i> , <i>Cladophora rupestris</i> , <i>Codium adhaerens</i> , <i>Codium fragile</i> , <i>Dictyosphaeria cavernosa</i> , <i>Monostroma hariotii</i> , <i>Valonia aegagropila</i>	[2,5,7,34,75]	<i>Ascophyllum nodosum</i> , <i>Desmarestia aculeata</i> , <i>Fucus spiralis</i> , <i>Halopteris scoparia</i> , <i>Padina crassa</i> , <i>Sargassum oligocystum</i>	[4,5,7,34,75]
UN	<i>Enteromorpha intestinalis</i> , <i>Prasiola stipitata</i> , <i>Prasiola crassa</i> ssp. antarctica	[2,75]	<i>Prasiola crassa</i>	[49]

Note: AS, Asterina-330; MG, Mycosporine-glycine; PE, Palythene; PL, Palythanol; PR, Porphyra-334; PI, Palythine; SH, Shinorine; UN, Unidentified MAAs.

Table 3. MAAs in macroalgal Rhodophytes.

MAAs	Red Macroalgae	Ref.
APA	<i>Agarophyton chilense</i> , <i>Bostrychia arbuscula</i> ^a , <i>Ceramium</i> sp. ^a , <i>Euptilota formosissima</i> ^a , <i>Gigartina macrocarpa</i> ^a , <i>Hymenena affinis</i> , <i>Mastocarpus stellatus</i> ^a , <i>Porphyra umbilicalis</i> ^a , <i>Pyropia columbina</i> ^a , <i>Pyropia plicata</i> ^a , <i>Rhodophyllis membranacea</i> ^a , <i>Sarcothalia atropurpurea</i> ^a , <i>Spongoconium pastorale</i> ^a	[71]
APB	<i>Agarophyton chilense</i> , <i>Champia novae-zelandiae</i> , <i>Gigartina macrocarpa</i> , <i>Porphyra umbilicalis</i> , <i>Pyropia columbina</i> , <i>Pyropia plicata</i> , <i>Sarcothalia atropurpurea</i>	[71]
AS	<i>Acanthophora muscoides</i> , <i>Acanthophora specifera</i> , <i>Agarophyton chilense</i> , <i>Amansia multifida</i> , <i>Ahmfeltiopsis devoniensis</i> , <i>Actinotrichia fragilis</i> , <i>Arthrocardia gardneri</i> , <i>Asparagopsis armata</i> , <i>Bangia atropurpurea</i> , <i>Bonnemaisonia hamifera</i> , <i>Bostrychia arbuscula</i> , <i>Bostrychia calliptera</i> , <i>Bostrychia montagnei</i> , <i>Bostrychia moritziana</i> , <i>Bostrychia radicans</i> , <i>Bostrychia scorpioides</i> , <i>Bostrychia simpliciuscula</i> , <i>Bryothamnion seaforthii</i> , <i>Bostrychia tenella</i> , <i>Bryothamnion triquetrum</i> , <i>Caloglossa apomeiatica</i> , <i>Caloglossa lepreurii</i> , <i>Calliarthron tuberculosum</i> , <i>Caloglossa stipitata</i> , <i>Caloglossa ogasawaraensis</i> , <i>Centroceras clavulatum</i> , <i>Ceramium nodulosum</i> , <i>Ceramium</i> sp., <i>Ceramium secundatum</i> , <i>Champia novae-zelandiae</i> , <i>Chondracanthus acicularis</i> , <i>Chondracanthus elegans</i> , <i>Chondracanthus teedei</i> , <i>Chondrus crispus</i> , <i>Chondrus ocellatus</i> , <i>Corallina officinalis</i> var. <i>chilensis</i> , <i>Corallina officinalis</i> , <i>Corallina</i> sp., <i>Corallina vancouveriensis</i> , <i>Craspedocarpus erosus</i> , <i>Cryptonemia crenulata</i> , <i>Curdiea racovitzae</i> , <i>Devaleraea ramentacea</i> , <i>Dichotomaria marginata</i> , <i>Digena simplex</i> , <i>Ellisolandia elongata</i> , <i>Euptilota formosissima</i> , <i>Gastroclonium ovatum</i> , <i>Gelidiella acerosa</i> , <i>Gelidiopsis variabilis</i> , <i>Gelidium amansii</i> , <i>Gelidium crinale</i> , <i>Gelidium corneum</i> , <i>Gelidium floridanum</i> , <i>Gelidium pusillum</i> , <i>Gelidium sesquipedale</i> , <i>Gloiopeltis furcata</i> , <i>Gigartina macrocarpa</i> , <i>Gigartina pistillata</i> , <i>Gigartina skottsbergii</i> , <i>Gracilaria caudata</i> , <i>Gracilaria changii</i> , <i>Gracilaria chilensis</i> , <i>Gracilaria cornea</i> , <i>Gracilaria conferta</i> , <i>Gracilaria euchaeumoides</i> , <i>Gracilaria domingensis</i> , <i>Gracilaria saliconia</i> , <i>Gracilaria tenuistipitata</i> , <i>Gracilaria vermiculophylla</i> , <i>Gracilariopsis longissima</i> , <i>Gracilariopsis tenuifrons</i> , <i>Gymnogongrus antarctica</i> , <i>Gymnogongrus antarcticus</i> , <i>Gymnogongrus griffithsiae</i> , <i>Hypnea musciformis</i> , <i>Hypnea spinella</i> , <i>Iridaea chordata</i> , <i>Jania adhaerens</i> , <i>Jania crassa</i> , <i>Jania cubensis</i> , <i>Jania rubens</i> , <i>Jania subulata</i> , <i>Kallymenia antarctica</i> , <i>Laurencia caraibica</i> , <i>Laurencia cartilaginea</i> , <i>Laurencia changii</i> , <i>Laurencia dendroidea</i> , <i>Laurencia filiformis</i> , <i>Laurencia obtusa</i> , <i>Lithophyllum incrustans</i> , <i>Lithophyllum expansum</i> , <i>Mastocarpus stellatus</i> , <i>Mazzaella flaccida</i> , <i>Mazzaella laminarioides</i> , <i>Myriogramme manginii</i> , <i>Notophycus fimbriatus</i> , <i>Osmundea hybrid</i> , <i>Osmundea pinnatifida</i> , <i>Osmundea spectabilis</i> , <i>Pachymenia laciniata</i> , <i>Palmaria decipiens</i> , <i>Palmaria palmata</i> , <i>Palisada flagellifera</i> , <i>Palisada perforata</i> , <i>Phyllophora appendiculata</i> , <i>Plocamium cartilagineum</i> , <i>Polysiphonia arctica</i> , <i>Porphyra endivifolium</i> , <i>Porphyra columbina</i> , <i>Porphyra leucosticta</i> , <i>Porphyra rosengurtii</i> , <i>Porphyra</i> ssp., <i>Prionitis lanceolata</i> , <i>Pterocladia capillacea</i> , <i>Pyropia acanthophora</i> , <i>Pyropia columbina</i> , <i>Pyropia plicata</i> , <i>Rhodophyllis membranacea</i> , <i>Rhodymenia pseudopalmata</i> , <i>Sarcothalia atropurpurea</i> , <i>Solieria filiformis</i> , <i>Spongoconium pastorale</i> , <i>Spyridia clavata</i> , <i>Stictosiphonia arbuscula</i> , <i>Stictosiphonia hookeri</i> , <i>Stictosiphonia intricate</i> , <i>Stictosiphonia tangatensis</i> , <i>Tricleocarpa cylindrica</i> , <i>Vertebrata lanosa</i>	[3–7,32,35,37,39–42,44,48,49,51,52,55,66,67,70,71,74,75,78–81,95–104]

Table 3. Cont.

MAAs	Red Macroalgae	Ref.
CL	<i>Catenella caespitosa</i> , <i>Catenella repens</i> , <i>Catenella nipae</i>	[49,72]
MAG	<i>Champia novae-zelandiae</i> , <i>Ceramium</i> sp., <i>Gigartina macrocarpa</i> , <i>Mastocarpus stellatus</i> , <i>Porphyra umbilicalis</i> , <i>Pyropia columbina</i> , <i>Pyropia plicata</i> , <i>Rhodophyllis membranacea</i> , <i>Sarcothalia atropurpurea</i> , <i>Spongoconium pastorale</i>	[78]
MG	<i>Acanthophora muscoides</i> , <i>Acanthophora specifera</i> , <i>Agarophyton chilense</i> , <i>Apophlaea lyallii</i> , <i>Blastophyllis calliblepharoides</i> , <i>Bostrychia moritziana</i> , <i>Bostrychia radicans</i> , <i>Bostrychia scorpioides</i> , <i>Centroceras clavulatum</i> , <i>Ceramium rubrum</i> , <i>Ceramium</i> sp., <i>Champia novae-zelandiae</i> , <i>Chondria arinata</i> , <i>Curdia racovitzae</i> , <i>Devaleraea ramentacea</i> , <i>Dumontia incrassata</i> ^a , <i>Gracilaria caudata</i> , <i>Gracilaria cornea</i> , <i>Grateloupia lanceola</i> , <i>Gymnogongrus turquetii</i> , <i>Hypnea spinella</i> , <i>Iridaea chordata</i> , <i>Jania subulata</i> , <i>Kallymenia antarctica</i> , <i>Laurencia caraibica</i> , <i>Laurencia caribica</i> , <i>Laminaria saccharina</i> , <i>Mazzaella laminarioides</i> , <i>Notophycus fimbriatus</i> , <i>Osmundaria obtusiloba</i> , <i>Pachymenia orbicularis</i> , <i>Palmaria decipiens</i> , <i>Palmaria palmata</i> , <i>Phyllophora antarctica</i> , <i>Phyllophora appendiculata</i> , <i>Porphyra columbina</i> , <i>Porphyra endiviifolium</i> , <i>Porphyra purpurea-violacea</i> , <i>Pyropia plicata</i> , <i>Rhodymenia</i> spp., <i>Sarcothalia atropurpurea</i> , <i>Schizymenia apoda</i> , <i>Spongoconium pastorale</i>	[2–7,32,34,35,37,40,42–45,55,69,71,74–78]
MMT	<i>Agarophyton chilense</i> , <i>Ceramium</i> sp., <i>Porphyra umbilicalis</i> , <i>Pyropia columbina</i> , <i>Pyropia plicata</i> , <i>Sarcothalia atropurpurea</i>	[77]
M2G	<i>Gloiopeltis furcata</i>	[40]
PE	<i>Acanthophora specifera</i> , <i>Actinotrichia fragilis</i> , <i>Agarophyton chilense</i> , <i>Bangia atropurpurea</i> , <i>Bostrychia simpliciuscula</i> , <i>Ceramium nodulosum</i> , <i>Chondrus crispus</i> , <i>Curdia racovitzae</i> , <i>Devaleraea ramentacea</i> , <i>Gigartina macrocarpa</i> , <i>Gracilaria changii</i> , <i>Gracilaria chilensis</i> , <i>Gracilaria tenuistipitata</i> , <i>Gracilariopsis tenuifrons</i> , <i>Gracilaria vermiculophylla</i> , <i>Iridaea chordata</i> , <i>Osmundea hybrid</i> , <i>Osmundea pinnatitida</i> , <i>Palmaria decipiens</i> , <i>Palmaria palmata</i> , <i>Phyllophora antarctica</i> , <i>Phyllophora appendiculata</i> , <i>Porphyra purpurea-violacea</i> , <i>Pyropia plicata</i> , <i>Rhodymenia pseudopalmata</i> , <i>Sarcothalia atropurpurea</i> , <i>Spongoconium pastorale</i> , <i>Stictosiphonia hookeri</i> , <i>Vertebrata lanosa</i>	[3–5,32,34,40–44,70,75,77,96,99,102,104]
PA	<i>Solieria chordalis</i>	[54]
PL	<i>Acanthophora specifera</i> , <i>Actinotrichia fragilis</i> , <i>Bangia atropurpurea</i> , <i>Bostrychia calliptera</i> , <i>Bostrychia montagnei</i> , <i>Bostrychia moritziana</i> , <i>Bostrychia radicans</i> , <i>Bostrychia simpliciuscula</i> , <i>Bostrychia tenella</i> , <i>Caloglossa lepreurii</i> , <i>Chondria arinata</i> , <i>Chondrus crispus</i> , <i>Corallina vancouveriensis</i> , <i>Curdia racovitzae</i> , <i>Devaleraea ramentacea</i> , <i>Ellisolandia elongata</i> , <i>Gelidium corneum</i> , <i>Gelidium pusillum</i> , <i>Gelidium sesquipedale</i> , <i>Gracilaria changii</i> , <i>Gracilaria chilensis</i> , <i>Gracilaria cornea</i> , <i>Gracilaria domingensis</i> , <i>Gracilaria eucheumoides</i> , <i>Gracilaria saliconia</i> , <i>Gracilaria tenuistipitata</i> , <i>Gracilariopsis longissima</i> , <i>Gracilariopsis tenuifrons</i> , <i>Halopythis incurve</i> , <i>Iridaea chordata</i> , <i>Kallymenia antarctica</i> , <i>Laurencia cartilaginea</i> , <i>Laurencia changii</i> , <i>Laurencia obtusa</i> , <i>Mazzaella flaccida</i> , <i>Mastocarpus stellatus</i> , <i>Osmundea spectabilis</i> , <i>Palmaria decipiens</i> , <i>Palmaria palmata</i> , <i>Plocamium cartilagineum</i> , <i>Polysiphonia arctica</i> , <i>Porphyra endiviifolium</i> , <i>Rhodymenia pseudopalmata</i> , <i>Rhodymenia</i> spp., <i>Stictosiphonia intricata</i> , <i>Stictosiphonia tangatensis</i>	[3–5,32,35,37,39–42,44,45,48,52,55,65,67,75,79,96–99,102,104,105]
PR	<i>Acanthophora muscoides</i> , <i>Acanthophora specifera</i> , <i>Actinotrichia fragilis</i> , <i>Agarophyton chilense</i> , <i>Amansia multifida</i> , <i>Arthrocardia gardneri</i> , <i>Asparagopsis armata</i> , <i>Asparagopsis taxiformis</i> , <i>Bangia atropurpurea</i> , <i>Bangia fuscopurpurea</i> , <i>Blastophyllis calliblepharoides</i> , <i>Bostrychia arbuscula</i> , <i>Bostrychia calliptera</i> , <i>Bostrychia harveyi</i> , <i>Bostrychia montagnei</i> , <i>Bostrychia moritziana</i> , <i>Bostrychia radicans</i> , <i>Bostrychia scorpioides</i> , <i>Bostrychia simpliciuscula</i> , <i>Bostrychia tenella</i> , <i>Bryothamnion seaforthii</i> , <i>Calliarthron tuberculosum</i> , <i>Caloglossa apomeiotta</i> , <i>Caloglossa lepreurii</i> , <i>Caloglossa ogasawaraensis</i> , <i>Caloglossa stipitata</i> , <i>Calliarthron tuberculosum</i> , <i>Catenella nipae</i> , <i>Ceramium nodulosum</i> , <i>Ceramium</i> sp., <i>Champia novae-zelandiae</i> , <i>Chondracanthus acicularis</i> , <i>Chondria arinata</i> , <i>Chondrus crispus</i> , <i>Corallina officinalis</i> , <i>Corallina officinalis</i> var. <i>chilensis</i> , <i>Corallina vancouveriensis</i> , <i>Craspedocarpus erosus</i> , <i>Curdia racovitzae</i> , <i>Cystoclonium purpureum</i> , <i>Devaleraea ramentacea</i> , <i>Dumontia incrassata</i> , <i>Endocladia muricata</i> , <i>Euptilota formosissima</i> , <i>Galaxaura oblongata</i> , <i>Ganonema farinosa</i> , <i>Gastroclonium ovatum</i> , <i>Gelidiella acerosa</i> , <i>Gelidiopsis variabilis</i> , <i>Gelidium amansii</i> , <i>Gelidium crinale</i> , <i>Gelidium corneum</i> , <i>Gelidium floridanum</i> , <i>Gelidium pusillum</i> , <i>Gelidium sesquipedale</i> , <i>Georgiella confluens</i> , <i>Gigartina macrocarpa</i> , <i>Gigartina skottsbergii</i> , <i>Gloiopeltis furcata</i> , <i>Gracilaria birdiae</i> , <i>Gracilaria caudata</i> , <i>Gracilaria changii</i> , <i>Gracilaria chilensis</i> , <i>Gracilaria conferta</i> , <i>Gracilaria cornea</i> , <i>Gracilaria domingensis</i> , <i>Gracilaria eucheumoides</i> , <i>Gracilaria saliconia</i> , <i>Gracilaria vermiculophylla</i> , <i>Gracilaria tenuistipitata</i> , <i>Grateloupia lanceola</i> , <i>Gymnogongrus griffithsiae</i> , <i>Halopythis incurve</i> , <i>Hymenena affinis</i> , <i>Hydropuntia cornea</i> , <i>Hypnea musciformis</i> , <i>Hypnea spinella</i> , <i>Iridaea</i> sp., <i>Iridaea chordata</i> , <i>Jania adhaerens</i> , <i>Jania rubens</i> , <i>Kallymenia antarctica</i> , <i>Laurencia caraibica</i> , <i>Laurencia cartilaginea</i> , <i>Laurencia changii</i> , <i>Laurencia dendroidea</i> , <i>Laurencia filiformis</i> , <i>Laurencia obtusa</i> , <i>Lithophyllum expansum</i> , <i>Lithophyllum incrustans</i> , <i>Lithothamnion antarcticum</i> , <i>Lithophyllum expansum</i> , <i>Mazzaella flaccida</i> , <i>Mastocarpus jardinii</i> , <i>Mastocarpus papillatus</i> , <i>Mastocarpus stellatus</i> , <i>Myriogramme manginii</i> , <i>Neuroglossum ligulatum</i> , <i>Nodularia spumigena</i> , <i>Notophycus fimbriatus</i> , <i>Osmundea hybrid</i> , <i>Osmundaria obtusiloba</i> , <i>Osmundea spectabilis</i> , <i>Pachymenia laciniata</i> , <i>Pachymenia orbicularis</i> , <i>Palmaria decipiens</i> , <i>Palmaria palmata</i> , <i>Palisada flagellifera</i> , <i>Palisada perforate</i> , <i>Pantoneura plocamioides</i> , <i>Plocamium cartilagineum</i> , <i>Phyllophora antarctica</i> , <i>Polysiphonia arctica</i> , <i>Porphyra dioica</i> , <i>Porphyra endiviifolium</i> , <i>Porphyra leucosticta</i> , <i>Porphyra plocamiestris</i> , <i>Porphyra purpurea</i> , <i>Porphyra purpurea-violacea</i> , <i>Porphyra rosenfurtii</i> , <i>Porphyra</i> sp., <i>Porphyra tenera</i> , <i>Porphyra umbilicalis</i> , <i>Porphyra yezoensis</i> , <i>Porphyra vietnamensis</i> , <i>Prionitis lanceolata</i> , <i>Pseudolithophyllum expansum</i> , <i>Pterocladia capillacea</i> , <i>Pterocladia</i> sp., <i>Ptilota plumosa</i> , <i>Pyropia acanthophora</i> , <i>Pyropia columbina</i> , <i>Pyropia plicata</i> , <i>Rhodophyllis membranacea</i> , <i>Rhodymenia pseudopalmata</i> , <i>Rhodymenia</i> spp., <i>Rhodymenia subantarctica</i> , <i>Sarcothalia atropurpurea</i> , <i>Schizymenia apoda</i> , <i>Scinaia boergesenii</i> , <i>Spongoconium pastorale</i> , <i>Spyridia clavata</i> , <i>Spyridia filamentosa</i> , <i>Stictosiphonia arbuscula</i> , <i>Stictosiphonia hookeri</i> , <i>Stictosiphonia intricata</i> , <i>Stictosiphonia tangatensis</i> , <i>Tricleocarpa cylindrical</i> , <i>Vertebrata lanosa</i>	[1,3–7,32,34,35,37,40–42,44,45,47,48,51,52,55,57,58,65–67,69,71,74–79,84–88,90–92,95,100,102,104–107]

Table 3. Cont.

MAAs	Red Macroalgae	Ref.
PI	<p><i>Acanthophora muscoides</i>, <i>Acanthophora specifera</i>, <i>Agarophyton chilense</i>, <i>Amansia multifida</i>, <i>Amphiroa rigida</i>, <i>Ahnfeltiopsis devoniensis</i>, <i>Arthrocardia gardneri</i>, <i>Asparagopsis armata</i>, <i>Asparagopsis taxiformis</i>, <i>Bangia atropurpurea</i>, <i>Blastophyllis calliblepharoides</i>, <i>Bonnemaisonia hamifera</i>, <i>Bostrychia arbuscula</i>, <i>Bostrychia calliptera</i>, <i>Bostrychia harveyi</i>, <i>Bostrychia moritziana</i>, <i>Bostrychia montagnei</i>, <i>Bostrychia pinnata</i>, <i>Bostrychia radicans</i>, <i>Bostrychia scorpioides</i>, <i>Bryothamnion seaforthii</i>, <i>Bostrychia tenella</i>, <i>Bryothamnion triquetrum</i>, <i>Calliarthron tuberculosum</i>, <i>Caloglossa ogasawaraensis</i>, <i>Centroceras clavulatum</i>, <i>Ceramium nodulosum</i>, <i>Ceramium secundatum</i>, <i>Ceramium sp.</i>, <i>Champia novae-zelandiae</i>, <i>Chondracanthus acicularis</i>, <i>Chondracanthus chamissoi</i>, <i>Chondracanthus elegans</i>, <i>Chondracanthus teedei</i>, <i>Chondria arinata</i>, <i>Chondrus crispus</i>, <i>Chondrus ocellatus</i>, <i>Chondrus yendoii</i>, <i>Corallina elongata</i>, <i>Corallina officinalis</i>, <i>Corallina officinalis</i> var. <i>chilensis</i>, <i>Corallina sp.</i>, <i>Corallina vancouveriensis</i>, <i>Craspedocarpus erosus</i>, <i>Cryptonemia crenulata</i>, <i>Curdia racovitzae</i>, <i>Devaleraea ramentacea</i>, <i>Dichotomaria marginata</i>, <i>Digenea simplex</i>, <i>Dumontia incrassata</i> ^a, <i>Ellisolandia elongata</i>, <i>Endocladia muricata</i>, <i>Euptilota formosissima</i>, <i>Gastroclonium ovatum</i>, <i>Gelidiella acerosa</i>, <i>Gelidiopsis variabilis</i>, <i>Gelidium amansii</i>, <i>Gelidium corneum</i>, <i>Gelidium crinale</i>, <i>Gelidium floridanum</i>, <i>Gelidium lingulatum</i>, <i>Gelidium pusillum</i>, <i>Gelidium sesquipedale</i>, <i>Georgiella confluens</i>, <i>Gigartina macrocarpa</i>, <i>Gigartina pistillata</i>, <i>Gigartina skottsbergii</i>, <i>Gracilaria asiatica</i>, <i>Gracilaria birdiae</i>, <i>Gracilaria caudata</i>, <i>Gracilaria changii</i>, <i>Gracilaria chilensis</i>, <i>Gracilaria conferta</i>, <i>Gracilaria cornea</i>, <i>Gracilaria domingensis</i>, <i>Gracilaria eucheumoides</i>, <i>Gracilaria saliconia</i>, <i>Gracilaria tenuistipitata</i>, <i>Gracilaria vermiculophylla</i>, <i>Gracilariopsis longissima</i>, <i>Grateloupia lanceola</i>, <i>Gymnogongrus Antarctica</i>, <i>Gymnogongrus antarcticus</i>, <i>Gymnogongrus griffithsiae</i>, <i>Halopythis incurve</i>, <i>Hymenena affinis</i>, <i>Hypnea musciformis</i>, <i>Hypnea spinella</i>, <i>Hypoglossum hypoglossoides</i>, <i>Iridaea chordata</i>, <i>Iridaea sp.</i>, <i>Jania adhaerens</i>, <i>Jania crassa</i>, <i>Jania cubensis</i>, <i>Jania rubens</i>, <i>Jania subulata</i>, <i>Kallymenia antarctica</i>, <i>Laurencia caraibica</i>, <i>Laurencia cartilaginea</i>, <i>Laurencia dendroidea</i>, <i>Laurencia filiformis</i>, <i>Laurencia obtusa</i>, <i>Lithophyllum incrustans</i>, <i>Lithophyllum expansum</i>, <i>Lithothamnion antarcticum</i>, <i>Lomentaria articulate</i>, <i>Mastocarpus jardinii</i>, <i>Mastocarpus stellatus</i>, <i>Mazzaella flaccida</i>, <i>Mazzaella laminarioides</i>, <i>Myriogramme manginii</i>, <i>Neuroglossum ligulatum</i>, <i>Notophycus fimbriatus</i>, <i>Osmundaria hybrid</i>, <i>Osmundaria obtusiloba</i>, <i>Osmundea pinnatitida</i>, <i>Osmundea spectabilis</i>, <i>Pachymenia laciniata</i>, <i>Pachymenia orbicularis</i>, <i>Palmaria decipiens</i>, <i>Palmaria palmata</i>, <i>Palisada flagellifera</i>, <i>Palisada perforata</i>, <i>Phyllophora antarctica</i>, <i>Phyllophora appendiculata</i>, <i>Plocamium cartilagineum</i>, <i>Polysiphonia arctica</i>, <i>Polysiphonia urceolata</i>, <i>Porphyra leucosticta</i>, <i>Porphyra purpurea-violacea</i>, <i>Porphyra rosenburgii</i>, <i>Porphyra sp.</i>, <i>Porphyra yezoensis</i>, <i>Porphyra umbilicalis</i>, <i>Prionitis lanceolata</i>, <i>Pterocladia capillacea</i>, <i>Pterocladia sp.</i>, <i>Pyropia columbina</i>, <i>Pyropia acanthophora</i>, <i>Pyropia plicata</i>, <i>Rhodophyllis membranacea</i>, <i>Rhodymenia pseudopalmata</i>, <i>Rhodymenia spp.</i>, <i>Sarcothalia atropurpurea</i>, <i>Sarcothalia papillosa</i>, <i>Schizymenia apoda</i>, <i>Scinaia boergesenii</i>, <i>Solieria filiformis</i>, <i>Solieria pacifica</i>, <i>Spongoconium pastorale</i>, <i>Stictosiphonia arbuscula</i>, <i>Stictosiphonia intricate</i>, <i>Stictosiphonia tangatensis</i>, <i>Tricleocarpa cylindrical</i>, <i>Vertebrata lanosa</i></p>	[3–7,32,34–37,39–46,48,50,52,55,56,58,65–71,75–79,82–84,90,91,95,97,100–102,108–110]
SH	<p><i>Acanthophora muscoides</i>, <i>Acanthophora spicifera</i>, <i>Actinotrichia fragilis</i>, <i>Agarophyton chilense</i>, <i>Ahnfeltiopsis devoniensis</i>, <i>Amansia multifida</i>, <i>Amphiroa rigida</i>, <i>Amphiroa sp.</i>, <i>Ahnfeltiopsis devoniensis</i>, <i>Arthrocardia gardneri</i>, <i>Asparagopsis armata</i>, <i>Asparagopsis taxiformis</i>, <i>Bangia atropurpurea</i>, <i>Bangia fuscopurpurea</i>, <i>Bangia sp.</i>, <i>Bonnemaisonia hamifera</i>, <i>Bostrychia arbuscula</i>, <i>Bostrychia calliptera</i>, <i>Bostrychia moritziana</i>, <i>Bostrychia montagnei</i>, <i>Bostrychia moritziana</i>, <i>Bostrychia scorpioides</i>, <i>Bostrychia simpliciuscula</i>, <i>Bostrychia tenella</i>, <i>Bryothamnion seaforthii</i>, <i>Bryothamnion triquetrum</i>, <i>Callithamnion tetragonum</i>, <i>Caloglossa apomeiatica</i>, <i>Caloglossa lepreurii</i>, <i>Caloglossa ogasawaraensis</i>, <i>Caloglossa stipitata</i>, <i>Calliarthron tuberculosum</i>, <i>Centroceras clavulatum</i>, <i>Ceramium echionotum</i>, <i>Ceramium nodulosum</i>, <i>Ceramium rubrum</i>, <i>Ceramium secundatum</i>, <i>Ceramium sp.</i>, <i>Champia novae-zelandiae</i>, <i>Chondracanthus acicularis</i>, <i>Chondracanthus chamissoi</i>, <i>Chondracanthus elegans</i>, <i>Chondracanthus teedei</i>, <i>Chondria arinata</i>, <i>Chondrus crispus</i>, <i>Chondrus yendoii</i>, <i>Corallina elongata</i>, <i>Corallina officinalis</i>, <i>Corallina officinalis</i> var. <i>chilensis</i>, <i>Corallina sp.</i>, <i>Corallina vancouveriensis</i>, <i>Craspedocarpus erosus</i>, <i>Cryptonemia crenulata</i>, <i>Curdia racovitzae</i>, <i>Cystoclonium purpureum</i> ^a, <i>Devaleraea ramentacea</i>, <i>Dichotomaria marginata</i>, <i>Digenea simplex</i>, <i>Dumontia incrassata</i> ^a, <i>Ellisolandia elongata</i>, <i>Endocladia muricata</i>, <i>Euptilota formosissima</i>, <i>Galaxaura oblongata</i>, <i>Ganonema farinosa</i>, <i>Gastroclonium ovatum</i>, <i>Gelidiella acerosa</i>, <i>Gelidiopsis variabilis</i>, <i>Gelidium amansii</i>, <i>Gelidium corneum</i>, <i>Gelidium crinale</i>, <i>Gelidium floridanum</i>, <i>Gelidium latifolium</i>, <i>Gelidium lingulatum</i>, <i>Gelidium pusillum</i>, <i>Gelidium sp.</i>, <i>Gelidium sesquipedale</i>, <i>Georgiella confluens</i>, <i>Gloiopeltis furcata</i>, <i>Gigartina macrocarpa</i>, <i>Gigartina pistillata</i>, <i>Gigartina skottsbergii</i>, <i>Gracilaria birdiae</i>, <i>Gracilaria caudata</i>, <i>Gracilaria cornea</i>, <i>Gracilaria changii</i>, <i>Gracilaria chilensis</i>, <i>Gracilaria conferta</i>, <i>Gracilaria cornea</i>, <i>Gracilaria domingensis</i>, <i>Gracilaria eucheumoides</i>, <i>Gracilaria gracilis</i>, <i>Gracilaria saliconia</i>, <i>Gracilaria tenuistipitata</i>, <i>Gracilaria vermiculophylla</i>, <i>Gracilariopsis longissima</i>, <i>Grateloupia doryphora</i>, <i>Gymnogongrus Antarctica</i>, <i>Gymnogongrus antarcticus</i>, <i>Gymnogongrus griffithsiae</i>, <i>Gymnogongrus turquetii</i>, <i>Halopythis incurve</i>, <i>Hypnea musciformis</i>, <i>Hypnea spinella</i>, <i>Hypoglossum hypoglossoides</i>, <i>Iridaea chordata</i>, <i>Iridaea sp.</i>, <i>Jania adhaerens</i>, <i>Jania crassa</i>, <i>Jania cubensis</i>, <i>Jania rubens</i>, <i>Jania subulata</i>, <i>Kallymenia antarctica</i>, <i>Laurencia caraibica</i>, <i>Laurencia changii</i>, <i>Laurencia dendroidea</i>, <i>Laurencia filiformis</i>, <i>Laurencia obtusa</i>, <i>Lithophyllum expansum</i>, <i>Lithophyllum incrustans</i>, <i>Lithophyllum expansum</i>, <i>Lithothamnion antarcticum</i>, <i>Lomentaria articulate</i>, <i>Mazzaella flaccida</i>, <i>Mazzaella laminarioides</i>, <i>Mastocarpus jardinii</i>, <i>Mastocarpus papillatus</i>, <i>Mastocarpus stellatus</i>, <i>Myriogramme manginii</i>, <i>Neuroglossum ligulatum</i>, <i>Notophycus fimbriatus</i>, <i>Osmundaria obtusiloba</i>, <i>Osmundea pinnatitida</i>, <i>Osmundea spectabilis</i>, <i>Pachymenia laciniata</i>, <i>Palmaria decipiens</i>, <i>Palmaria palmata</i>, <i>Palisada flagellifera</i>, <i>Palisada perforata</i>, <i>Pantoneura plocamioides</i>, <i>Phyllophora antarctica</i>, <i>Phyllophora appendiculata</i>, <i>Plocamium cartilagineum</i>, <i>Polysiphonia arctica</i>, <i>Porphyra dioica</i>, <i>Porphyra endiviifolium</i>, <i>Polysiphonia urceolata</i>, <i>Porphyra haitanensis</i>, <i>Porphyra leucosticta</i>, <i>Porphyra plocamiestris</i>, <i>Porphyra purpurea</i>, <i>Porphyra rosenburgii</i>, <i>Porphyra sp.</i>, <i>Porphyra umbilicalis</i>, <i>Porphyra yezoensis</i>, <i>Prionitis lanceolata</i>, <i>Pseudolithophyllum expansum</i> ^a, <i>Pterocladia lucida</i>, <i>Pterocladia capillacea</i>, <i>Pterocladia sp.</i>, <i>Pyropia acanthophora</i>, <i>Pyropia columbina</i>, <i>Pyropia plicata</i>, <i>Rhodomela virgata</i>, <i>Rhodophyllis membranacea</i>, <i>Rhodymenia pseudopalmata</i>, <i>Rhodymenia spp.</i>, <i>Rissoella verruculosa</i>, <i>Sarcothalia atropurpurea</i>, <i>Sarcothalia papillosa</i>, <i>Schizymenia apoda</i>, <i>Scinaia boergesenii</i>, <i>Spongoconium pastorale</i>, <i>Spyridia clavata</i>, <i>Stictosiphonia arbuscula</i>, <i>Stictosiphonia hookeri</i>, <i>Stictosiphonia intricate</i>, <i>Stictosiphonia tangatensis</i>, <i>Trichocarpus crinitus</i>, <i>Tricleocarpa cylindrical</i></p>	[1,3–7,32,34–40,42–45,48,50–53,55–57,66–68,70,71,75–79,82,84–86,90–92,96,98,101,103,105,108,110–113]

Table 3. Cont.

MAAs	Red Macroalgae	Ref.
US	<i>Agarophyton chilense</i> , <i>Bostrychia scorpioides</i> , <i>Calliarthron tuberculatum</i> , <i>Ceramium nodulosum</i> , <i>Ceramium</i> sp., <i>Chondracanthus acicularis</i> , <i>Corallina officinalis</i> var. <i>chilensis</i> , <i>Corallina vancouveriensis</i> , <i>Gigartina macrocarpa</i> , <i>Gracilariopsis tenuifrons</i> , <i>Gracilaria vermiculophylla</i> , <i>Mastocarpus papillatus</i> , <i>Mastocarpus stellatus</i> , <i>Mazzaella flaccida</i> , <i>Osmundea hybrid</i> , <i>Osmundea pinnatifida</i> , <i>Palmaria decipiens</i> , <i>Palmaria palmata</i> , <i>Phyllophora Antarctica</i> , <i>Prionitis lanceolata</i> , <i>Pterocladia capillacea</i> , <i>Pyropia plicata</i> , <i>Rhodophyllis membranacea</i> , <i>Rhodymenia pseudopalmeta</i> , <i>Sarcothalia atropurpurea</i> , <i>Spongoconium pastorale</i> , <i>Vertebrata lanosa</i>	[4,6,37,39,52,55,70,76–78,104]
NM	<i>Bostrychia scorpioides</i> , <i>Gracilaria vermiculophylla</i>	[70,71]
UN	<i>Ahnfeltiopsis devoniensis</i> I–II, <i>Asparagopsis armata</i> , <i>Bonnemaisonia hamifera</i> , <i>Bostrychia calliptera</i> , <i>Bostrychia scorpioides</i> I–II, <i>Bostrychia</i> sp., <i>Callithamnion tetragonum</i> , <i>Callophyllis variegata</i> , <i>Catenella caespitosa</i> I–II, <i>Catenella nipae</i> I–IX, <i>Catenella impudica</i> , <i>Catenella repens</i> I–II, <i>Ceramium nodulosum</i> I–II, <i>Ceramium rubrum</i> , <i>Ceramium secundatum</i> I–II, <i>Chondracanthus acicularis</i> I–II, <i>Chondria arinata</i> , <i>Chondrus crispus</i> I–II, <i>Chondrus ocellatus</i> , <i>Corallina officinalis</i> , <i>Corallina</i> sp. I–II, <i>Curdia racovitzae</i> I–II, <i>Devaleraea ramentacea</i> , <i>Gastroclonium ovatum</i> , <i>Gelidium corneum</i> I–II, <i>Gigartina pistillata</i> I–II, <i>Gigartina skottsbergii</i> , <i>Gigartina skottsbergii</i> , <i>Gracilaria changii</i> , <i>Gracilaria conferta</i> , <i>Gracilaria gracilis</i> , <i>Gracilaria lemaneiformis</i> I–II, <i>Gracilaria vermiculophylla</i> I–III, <i>Gracilariopsis longissima</i> , <i>Gracilariopsis tenuifrons</i> , <i>Hypoglossum hypoglossoides</i> , <i>Iridaea chordata</i> , <i>Iridaea tuberculosa</i> , <i>Iridaea cordata</i> , <i>Kallymenia antarctica</i> , <i>Lophurella hoockeriana</i> , <i>Mazzaella laminarioides</i> , <i>Mastocarpus stellatus</i> I–II, <i>Myriogramme manginii</i> , <i>Neuroglossum ligulatum</i> , <i>Nothogenia fastigiata</i> , <i>Notophycus fimbriatus</i> , <i>Nothogenia</i> sp., <i>Osmundea hybrid</i> , <i>Osmundea pinnatifida</i> , <i>Palmaria decipiens</i> , <i>Palmaria palmata</i> I–III, <i>Phyllophora truncata</i> , <i>Polysiphonia arctica</i> , <i>Polysiphonia</i> sp., <i>Porphyra dioica</i> , <i>Porphyra endiviifolium</i> , <i>Porphyra rosenfurtii</i> , <i>Porphyra</i> spec., <i>Porphyra yezoensis</i> , <i>Pseudolithophyllum expansum</i> , <i>Ptilota gunneri</i> , <i>Ptilonia magellanica</i> , <i>Pyropia columbina</i> , <i>Rhodomela confervoides</i> , <i>Sarcothalia crispata</i> , <i>Sarcothalia papillosa</i> , <i>Schizoseris</i> sp., <i>Solieria chordalis</i> , <i>Vertebrata lanosa</i>	[1,3,4,6,7,37,40,44,47,54,57,69,70,75,86,88,90,102,105,114,115]

Note: APA, Aplysiapalythine A [^a. Tentative identification]; APB, Aplysiapalythine B; AS, Asterina-330; CL, Catenelline; MAG, mycosporine-alanine-glycine; MG, Mycosporine-glycine; MMT, mycosporine-methylamine-threonine; M2G, Mycosporine-2-glycine; PE, Palythene; PA, Palythenic acid; PI, Palythine; PL, Palythinol; PR, Porphyra-334; PS, Palythine-serine; SH, Shinorine; SME, Shinorine methyl ester; US, Usujirene; NM, Novel MAAs; UN, Unidentified MAAs.

2.2. An Open Database for MAAs in Marine Macroalgae

In order for the scientists in the field to have a more comprehensive and clearer understanding of MAAs in marine macroalgae, it was necessary to establish a corresponding database. Therefore, our project team established a database (<http://210.28.32.218/MAAs/>) of MAAs in marine macroalgae over the past nearly 30 years utilizing data information from the Web of Science, Springer, Google Scholar and CNKI. In this database, more detailed information in relation to algal MAAs, such as the total contents of MAAs, content of specific MAA, type of MAAs, origin of marine macroalgae, and/or composition of specific MAA in MAAs, was listed. This was the comprehensive summary database of MAAs in marine macroalgae at home and abroad, and it was open and free.

Up to now, it has been determined that 572 species of marine macroalgae contained MAAs. Among them, MAAs contents and/or MAAs composition in 501 species have been reported. Therefore, related informations of MAAs in 501 species of marine macroalgae since 1990 have been gotten using our database for MAAs in marine macroalgae. In the following work process, we will try to expand the sources of the reports collection and its published time in order to provide more complete data about MAAs in marine macroalgae.

2.3. Marine Macroalgae with No Detectable MAAs Concentrations

MAAs accumulation in marine macroalgae were widespread and but not ubiquitous characteristics, and some marine macroalgae did not contain MAAs with detectable concentrations. We found that these marine macroalgae distributed in 18 orders (Figure 6) and its numbers were more than 100 species (Table 4) in the past 30 years. From Figure 6 it appeared that marine macroalgae with no detectable MAA concentrations have a wide taxonomic distribution.

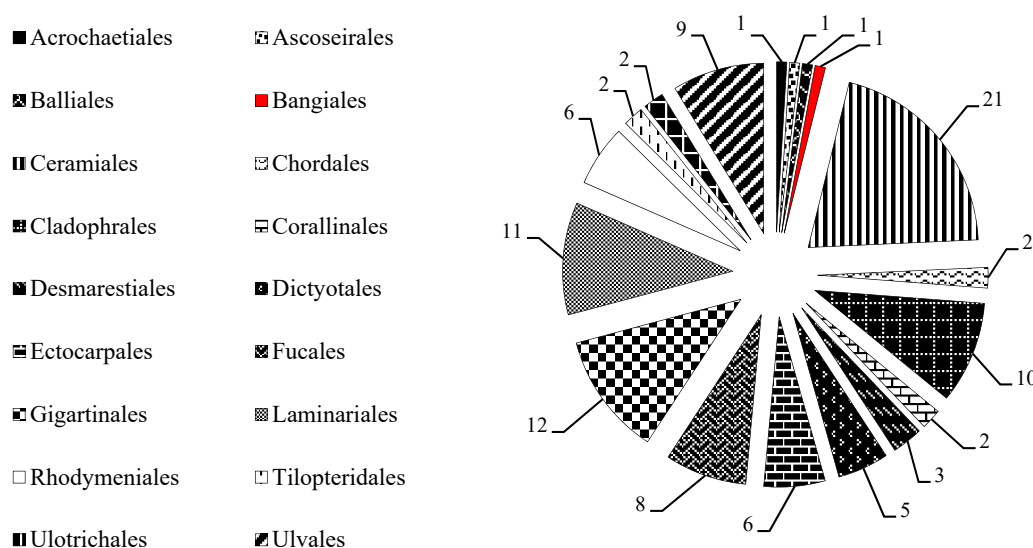


Figure 6. Distribution of marine macroalgae with no detectable MAAs concentrations. Data collected from related studies since 1990, and the number in a pie chart represents the number of marine macroalgae belonging to these orders.

Table 4. Marine macroalgae with no detectable MAAs concentrations.

Marine Macroalgae	
Chlorophyta	<i>Acrosiphonia arcta</i> [3], <i>Acrosiphonia penicilliformis</i> [3], <i>Anadyomene wrightii</i> [3], <i>Boergesenia forbesii</i> [3], <i>Chaetomorpha linum</i> [3], <i>Chaetomorpha melagonium</i> [3], <i>Cladophora rupestris</i> [3], <i>Enteromorpha compressa</i> [3], <i>Enteromorpha intestinalis</i> [3], <i>Enteromorpha</i> sp. [3], <i>Enteromorpha</i> spp. [3], <i>Monostroma nitidum</i> [3], <i>Monostroma arcticum</i> [3], <i>Ulva conglohata</i> [3], <i>Ulva fasciata</i> [3], <i>Ulva lactuca</i> [3], <i>Ulva olivascens</i> [3], <i>Ulva rotundata</i> [3], <i>Valoniopsis pachynema</i> [3]
Phaeophyta	<i>Adenocystis utricularis</i> [3], <i>Alaria esculenta</i> [3], <i>Ascoseira mirabilis</i> [3], <i>Chnoospora implexa</i> [3], <i>Chorda filum</i> [3], <i>Chordaria flagelliformis</i> [3], <i>Colpomenia sinuosa</i> [3], <i>Cystoseira usneoides</i> [3], <i>Desmarestia aculeata</i> [3], <i>Desmarestia menziesii</i> [3], <i>Dictyota dichotoma</i> [3], <i>Fucus distichus</i> [3], <i>Fucus serratus</i> [3], <i>Fucus spiralis</i> [3], <i>Fucus vesiculosus</i> [3], <i>Kjellmaniella crassifolia</i> [3], <i>Laminaria digitata</i> [3], <i>Laminaria hyperborean</i> [3], <i>Laminaria japonica</i> [3], <i>Laminaria ochroleuca</i> [3], <i>Laminaria saccharina</i> [3], <i>Laminaria solidungula</i> [3], <i>Padina boryana</i> [3], <i>Padina pavonica</i> [3], <i>Phaeurus antarcticus</i> [3], <i>Saccorhiza dermatodea</i> [3], <i>Saccorhiza polyschides</i> [3], <i>Sargassum muticum</i> [3]
Rhodophyta	<i>Antarcticothamnion polysporum</i> [3], <i>Audouinella purpurea</i> [3], <i>Ballia callitricha</i> [3], <i>Bornetia secundiflora</i> [70], <i>Calliblepharis jubata</i> [70], <i>Callithamnion tetragonum</i> [70], <i>Champia parvula</i> [70], <i>Chylocladia verticillata</i> [70], <i>Delesseria lancifolia</i> [3], <i>Delesseria sanguinea</i> [3], <i>Dilsea carnosa</i> [76], <i>Furcellaria lumbricalis</i> [3,76], <i>Griffithsia corallinoides</i> [70], <i>Hymenocladopsis crustigena</i> [3], <i>Heterosiphonia plumosa</i> [70], <i>Membranoptera alata</i> [70], <i>Metacallophyllis laciniata</i> [70], <i>Myriogramme smithii</i> [3], <i>Odonthalia dentate</i> [4], <i>Pantoneura plocamioides</i> [3], <i>Phyllophora ahmfeltioides</i> [3], <i>Phycodrys austrogeorgica</i> [3], <i>Phycodrys rubens</i> [3,71], <i>Phycodrys quercifolia</i> [3], <i>Phyllophora truncata</i> [3], <i>Picconiella plumosa</i> [3], <i>Plocamium cartilagineum</i> [3], <i>Plumaria plumosa</i> [70], <i>Porphyra plocamiestris</i> [3], <i>Ptilota serrate</i> [3], <i>Polysiphonia elongata</i> [3], <i>Polyides rotundus</i> [3], <i>Sphaerococcus coronopifolius</i> [70]

The green algae (21 species) in Chlorophyta, the brown algae (37 species) in Phaeophyta, and the red algae (45 species) in Rhodophyta were confirmed to have no detectable MAAs concentrations (Table 4), such as macroalgal Chlorophytes *Acrosiphonia arcta* [3], *Acrosiphonia penicilliformis* [3], *Anadyomene wrightii* [3], and etc. [3]; macroalgal Phaeophytes *Adenocystis utricularis* [3], *Alaria esculenta* [3], *Ascoseira mirabilis* [3], and others brown algae [3]; macroalgal Rhodophytes *Antarcticothamnion polysporum* [3], *Heterosiphonia plumosa* [70], *Odonthalia dentate* [4], and so on [3,70].

MAAs were an important class of bioactive secondary metabolites in marine macroalgae [67,68], their types and accumulation were variable with some environmental variables, including radiation [6,74,77,81,116], nutrients [6,74,77,81], salinity [44], temperature [116], and desiccation [113,117]. These studies were not included in this paper.

crispus [41,57], *Gelidium corneum* [39,129], *Gelidium lingulatum* [50], *Gracilaria changii* [108,130], *Gracilaria cornea* [87], *Mastocarpus stellatus* [76,77], *Palmaria decipiens* [123], *Palmaria palmata* [57,131], *Porphyra dioica* [57], *Porphyra rosengurttii* [39,119], *Porphyra* sp. [32,131], *Porphyra tenera* [123,132], *Porphyra yezoensis* [76,77,105,128], *Pyropia leucosticta* [39] and *Pyropia plicata* [104], such as palythine, palythinol, shinorine, usujirene and *etc.*, that were often used as standards for identification and quantification of MAAs, also have been researched. The extraction process of MAAs in *Eucheuma* [124,133], *Gloiopeltis furcata* [51], *Gracilaria chilensis* [105], *Porphyra* sp., [134,135], *Porphyra haitanensis* [135] and *Porphyra yezoensis* [136] has been pointed. Therefore, the purification and preparation of MAAs in marine macroalgae need to be explored in future studies.

3. Materials and Methods

3.1. Methods

Utilizing data obtained from the Web of Science, Springer, Google Scholar, and CNKI, the reliable material sources of this systematic manuscript paper were obtained from literature published during the last thirty years. Further, to provide more explicit knowledge, the development tendency of the studies about MAAs in marine macroalgae has been analyzed by using CiteSpace (4.0) [60]. Corresponding data on MAAs in marine macroalgae was extracted from related studies collected using the Web of Science during 2009 and 2019 years.

3.2. Total MAAs Contents and Specific MAA Concentration

In this work, total MAAs content and/or specific MAA concentration in each marine macroalgae species was not clearly listed, however, they were obtained using an online database (<http://210.28.32.218/MAAs/>), which was built by our team. A great deal of reports which were collected from the Web of Science, Springer, Google Scholar, and CNKI were built for this database.

4. Conclusions

This review summed up the basic situation of MAAs in 572 species of marine macroalgae which belonged to 28 orders, from 1990 to 2019, in particular, 45 species in Chlorophyta, 41 species in Phaeophyta, and 486 species in Rhodophyta, and found the existence of 22 fully characterized MAAs and a large number of unidentified MAA(s) in them. Five MAAs, namely shinorine, porphyra-334, palythine, asterina-330, and palythinol were the most common in Rhodophytes, followed by mycosporine-glycine, palythene, and usujirene. Among them, seven MAAs, including asterina-330, mycosporine-glycine, palythene, palythinol, porphyra-334, palythine, and shinorine, were found in Chlorophytes and Phaeophytes. In addition, so far, aplysiapalythine A, aplysiapalythine B, catenelline, prasiolin and bostrychines A–F only have been found in Rhodophytes. According to different orders of marine macroalgae, the total MAAs contents in 12 species macroalgal Chlorophytes, 8 species macroalgal Phaeophytes and 323 species macroalgal Rhodophytes were pointed out in this work. Meanwhile, we detailed the structure, extinction coefficient, retention time, and maximum absorption wavelength of 10 common MAAs.

Further, an open online database (<http://210.28.32.218/MAAs/>) for MAAs in 501 species of marine macroalgae was established on data mentioned above to quickly retrieve information related to MAAs in marine macroalgae since 1990. In this database, the source (field/culture) and collection site of marine macroalgae, total MAAs content, MAA type and/or content have been listed.

Finally, the studies about MAAs in marine macroalgae were analyzed using CiteSpace considering the past 10 years, and the result demonstrated that the purification and preparation of MAA purified standards from marine macroalgae constitute a domain worthy to be penetratingly explored in future studies.

In order to gain better knowledge about the current states and progress of MAAs in marine macroalgae, more reports have to be collected regarding MAAs from other sources of data. Overall,

based on data from the last 30 years, our work provided more a comprehensive reference and fast inquiry about MAAs in marine macroalgae for relevant researchers.

Author Contributions: Software, Y.S.; investigation, N.Z. and X.Z.; data curation, N.Z.; writing—original draft preparation, Y.S.; writing—review and editing, Y.S. and J.Z.; visualization, Y.S. and N.Z.; supervision, L.G. and G.G.; project administration, Y.S. and S.D. All authors have read and agreed to the published version of the manuscript.

Funding: This work was supported by the Open Project Program of State Key Laboratory of Food Science and Technology, Jiangnan University (SKLF-KF-201904); Supported by Natural Science Fund for Colleges and Universities in Jiangsu Province (19KJA430010); the Priority Academic Program Development of Jiangsu Higher Education Institutions; Special Foundation for Excellent Young Teachers and Principals Program of Jiangsu Province, China; and Postgraduate Research and Innovation Plan Project in Jiangsu Province (SJCX19_1002).

Conflicts of Interest: The authors declare no conflict of interest.

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