Occurrence of Photoprotective Mycosporine-like Amino Acid Compounds (MAAs) in Marine Red Macroalgae from Temperate Australian Waters

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UV-absorbing mycosporine-like amino acid compounds (MAAs) were identified and quantified in 35 red macroalgal species (Rhodophyta) collected from the rocky shores of Southeastern New South Wales and Southern Victoria, Australia. Within all taxa investigated 5 distinct compounds were found, which were identified as shinorine, porphyra-334, palythine, asterina-330 and palythinol. While sublittoral species contained only trace amounts of MAAs or even lack these substances, intertidal plants always exhibited high concentrations. The data suggest that the biosynthesis and accumulation of MAAs may represent a natural defence system against exposure to biologically harmful UV-radiation.

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KEYWORDS: mycosporine-like amino acid compounds, MAAs, macroalgae, UV-radiation

INTRODUCTION

Due to a decrease in stratospheric ozone, levels of ultraviolet B (UVB, 280-320 nm) reaching the Earth's surface had increased by >50% in Antarctica under spring "ozone hole" conditions (Madronich et al. 1998). This depleted ozone layer does usually not extend as far north as Australia, but stratospheric winds can occasionally carry ozone-depleted air masses towards Australia causing a short term rise in UVB values. Although the relative rise in UVB has been most pronounced in the polar regions over the last decade (Kerr 1994), high ambient doses of UV-radiation are characteristic of tropical/subtropical continents such as Australia even under normal stratospheric ozone concentrations (Fleischmann 1989). In these regions, the light path for solar radiation is short and the usually clear, oligotrophic water column exhibits a high transparency for UVB (Smith and Baker 1979). Consequently, many phototrophic organisms in aquatic ecosystems may be affected by this spectral waveband (Franklin and Forster 1997).

Multiple harmful effects of UVB on marine primary producers have been reported, and include the direct influences on molecular targets such as nucleic acids and proteins, on physiological processes such as photosynthesis, growth and on community structures (Smith et al. 1992; Buma et al. 1995; Davidson et al. 1996; Franklin and Forster 1997; Aquilera et al. 1999). Of major interest is the identification of repair and/or protective mechanisms that allow phototrophic organisms living in high-light habitats to survive and reproduce.

An important physiochemical mechanism against biologically harmful UV-radiation involves the biosynthesis and accumulation of photoprotective sunscreens. Typically absorbing in the UVA (320-400 nm) and UVB, these compounds were invoked to function as passive shielding substances by dissipating the absorbed radiation energy in form of harmless heat without generating photochemical reactions (Bandaranayake 1998).

The most common substances with a potential role as UV-sunscreens in marine organisms are the mycosporine-like amino acids (MAAs), a suite of chemically closely related, water-soluble compounds. MAAs have been identified in taxonomically diverse marine organisms including bacteria, cyanobacteria, micro- and macroalgae, invertebrates and fish (Dunlap and Shick 1998). Their function as intracellular screening agents has been inferred from a decrease in concentration with increasing depth as observed in corals (Dunlap et al. 1986) and macroalgae (Karsten et al. 1999). In addition, macroalgae from South Europe contain up to 2-fold higher MAA contents compared to similar species from higher latitudes indicating a positive relationship with the natural solar UV-radiation of the respective biogeographic region, i.e. the higher the UV-dose the more MAAs are formed and accumulated (Karsten et al. 1998a). In more recent studies on microalgae, Riegger and Robinson (1997) calculated sunscreen factors for Antarctic phytoplankton due to the presence of MAAs of up to 0.72, i.e. 72% of harmful UV quanta were absorbed before hitting intracellular molecular targets. In the red-tide dinoflagellate *Gymnodinium sanguineum* Hirasaka, MAAs prevent, at least partially, UV-induced inhibition of photosynthesis (Neale et al. 1998).

Although MAAs are widely present in various types of marine organisms, few data exist of their type and quantity in macroalgae (Nakamura et al. 1982; Karentz et al. 1991; Karsten et al. 1998a,b), in particular from high-radiation coasts such as in Australia. In the present investigation a qualitative and quantitative inventory was made of MAAs in red macroalgae collected from the rocky shore in southeastern New South Wales and southern Victoria.

MATERIALS AND METHODS

The locations of collection in southeastern New South Wales and southern Victoria are shown in Figure 1 and the red macroalgal species studied are listed in Table 1. All plants were sampled during a field trip in March 1999 directly from the shore as attached or drift material, or by snorkeling. Afterwards the algae were air-dried in the sun followed by storage in sealed plastic bags under cool, dry and dark conditions until analysis.

Thalli of about 10-20 mg dry weight (DW) were extracted for 2 h in screw-capped centrifuge vials filled with 1 mL 25% aqueous methanol (v/v) and incubated in a waterbath at 45°C. After centrifugation at 5000 g for 5 min, 700 µL of the supernatants were evaporated to dryness under vacuum (Speed Vac Concentrator SVC 100H). Dried extracts were re-dissolved in 700 µL 100% methanol and vortexed for 30 s. After passing through a 0.2 µm membrane filter, samples were analysed with a Waters HPLC system according to the method of Karsten et al. (1998a), modified as follows. MAAs were separated on a stainless-steel Phenomenex Sphereclone RP-8 column (5 µm, 250 x 4 mm I.D.) protected with a RP-8 guard cartridge (20 x 4 mm I.D.). The mobile phase was 5% aqueous methanol (v/v) plus 0.1% acetic acid (v/v) in water, run isocratically at a flow rate of 0.7 ml min^{-1}. MAAs were detected at 330 nm and absorption spectra (290-400 nm) were recorded each second directly on the HPLC-separated peaks. Identification was done by spectra, retention time and by co-chromatography with standards extracted from the marine red macroalgae *Chondrus crispus* Stackhouse (Karsten et al., 1998a) and *Porphyra umbilicalis* (Linnaeus) Kützing, as well as from ocular lenses of the coral trout *Plectropomus leopardus* (Lacepède, 1802), kindly sent by Dr. David Bellwood, James Cook University, Townsville, Australia. Quantification was made using the following molar extinction coefficients: shinorine: e334=44,700 (Tsujino et al. 1980), palythine: e320=36,200 (Takano et al. 1978), palythinol: e332=43,500 (Dunlap et al. 1986), porphyra-334: e334=43,300 (Takano et al. 1978),

asterina-330: e330=43,500 (Gleason 1993). All amounts are given as mean of 4 replicates (±SD) based on separate extracts from separate algae, randomly collected from the respective habitat and expressed as concentration on a dry weight basis.

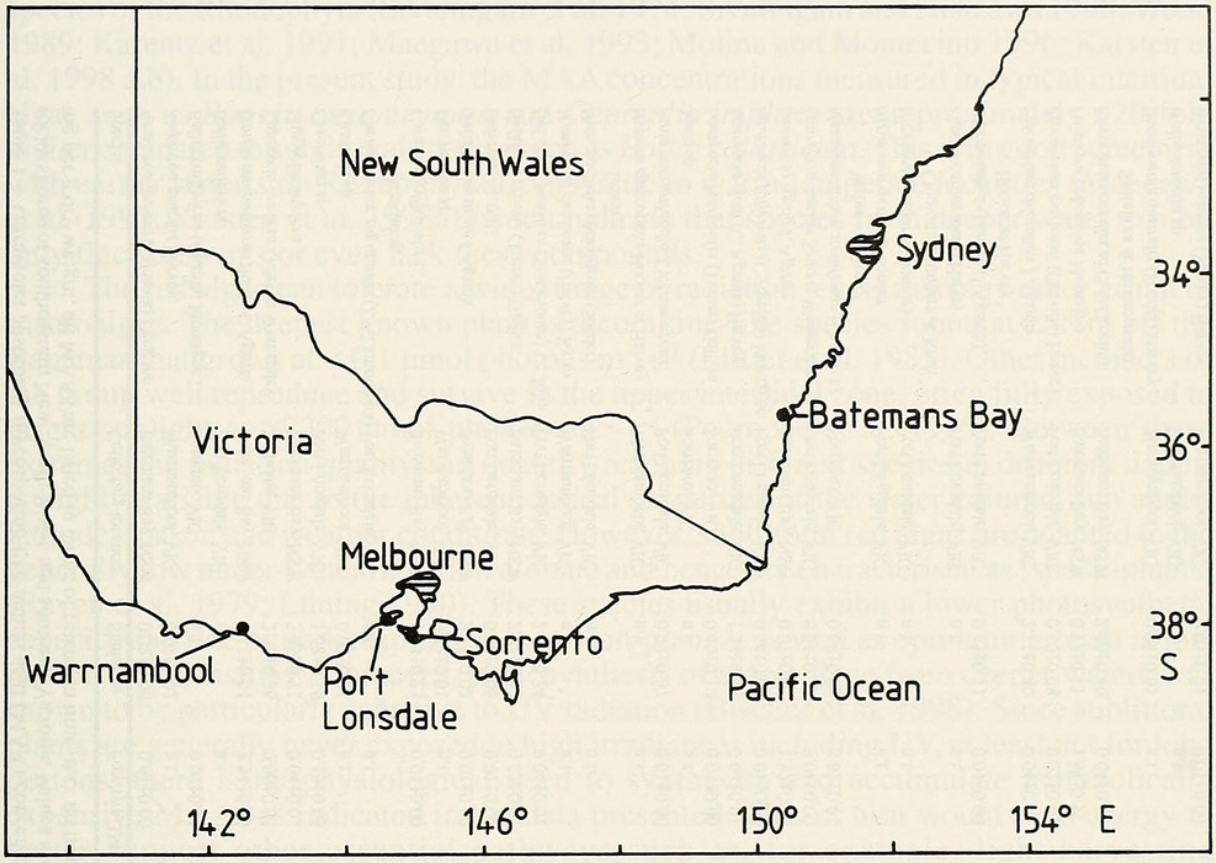

FIGURE LEGENDS

Figure 1. Map showing collecting location in southeastern New South Wales and southern Victoria, Australia.

RESULTS

The MAAs extracted from the dried red algal samples were characterised by HPLC, and identified and quantified according to their retention times, absorption spectra, co-chromatography with standards and molar extinction coefficients (see Materials and Methods). Five different MAAs could be detected within the samples investigated, all of which were identified as shinorine, porphyra-334, palythine, asterina-330 and palythinol (Table 1). The sum of all MAAs ranged in all macroalgae analysed from 0 (no trace) to 5.5 mg g^{-1} DW. While typical subtidal species such as *Ballia callitrichia, Hypnea episcopalis*, *Nizymenia australis* and *Phacelocarpus alatus* contained no MAAs at all or traces only, intertidal species such as *Bangia atropurpurea*, *Capreolia implexa*, *Gelidium australe* and *Porphyra columbina* exhibited high MAA concentrations between approximately 2.5 and 5.5 mg g^{-1} DW (Table 1). Quantitatively asterina-330 and palythinol played a minor role as indicated by low maximum concentrations of 0.38 mg g^{-1} DW as detected in *Laurencia elata*. While palythine showed high contents of up to 1.7 mg g^{-1} DW in only few species such as *L. elata*, shinorine was the quantitatively dominant MAA in most species containing this compound. The maximum amounts of shinorine reached up to 3.9 mg g^{-1} DW. Porphyra-334 occurred in high concentrations between 1.5 and 2.5 mg g^{-1} DW in *Bangia atropurpurea*, *Laurencia rigida* and *Porphyra columbina* (Table 1).

Table 1 – Ultraviolet absorbing mycosporine-like amino acid (MAA) concentrations in red macroalgae collected in March 1999 from the rocky shores of southeastern New South Wales and southern Victoria. Values are given as mean ± standard deviation (n=4) and expressed as mg per g dry weight; all MAAs are listed in terms of retention time. n.t.: no trace.

Species	Collecting location	Shinorine	Porphyra-334	Palythine	Asterina-330	Palythinol	ΣMAAs
Amphiroa anceps (Lamarck) Decaisne	Batemans Bay, NSW	0.22±0.06	0.01±0.00	n.t.	n.t.	n.t.	0.23±0.01
Amphiroa gracilis Harvey	Warrnambool, VIC	0.07±0,02	n.t.	n.t.	n.t.	n.t.	0.07±0.02
Ballia callitricha (Agardh) Montagne	Sorrento, VIC	n.t.	0.02±0.01	n.t.	n.t.	n.t.	0.01±0.01
Ballia callitricha	Port Lonsdale, VIC	n.t.	n.t.	0.01±0.00	n.t.	n.t.	0.01±0.00
Bangia atropurpurea (Roth) C.Agardh	Batemans Bay, NSW	0.11±0.01	2.54±0.29	0.03±0.01	n.t.	n.t.	2.68±0.31
Capreolia implexa Guiry et Womersley	Sorrento, VIC	2.36±0.36	0.06±0.03	0.79±0.13	0.14±0.02	n.t.	3.36±0.52
Capreolia implexa	Batemans Bay, NSW	3.85±0.71	0.04±0.01	1.33±0.13	0.24±0.03	0.04±0.01	5.48±0.73
Ceramium sp.	Port Lonsdale, VIC	1.68±0.36	0.16±0.06	0.67±0.25	0.06±0.02	n.t.	2.57±0.49
Champia sp.	Warrnambool, VIC	0.02±0.01	n.t.	0.02±0.01	0.01±0.00	n.t.	0.04±0.02
Cheilosporum sagittatum (J.V.Lamouroux) Areschoug,	Port Lonsdale, VIC	n.t.	n.t.	n.t.	n.t.	n.t.	n.t.
Corallina officinalis L.	Batemans Bay, NSW	1.03±0.23	0.01±0.00	0.09±0.03	0.01±0.00	n.t.	1.14±0.26
Dictymenia sp.	Warrnambool, VIC	0.02±0.01	n.t.	0.01±0.00	n.t.	n.t.	0.03±0.01
Gelidium australe J.Agardh	Batemans Bay, NSW	2.15±0.02	0.01±0.00	0.01±0.00	0.01±0.00	n.t.	2.18±0.02
Gelidium australe	Port Lonsdale, VIC	0.90±0.06	0.01±0.00	1.00±0.04	0.15±0.01	n.t.	2.05±0.03
Gelidium crinale (Turner) Gaillon	Batemans Bay, NSW	2.92±0.23	0.02±0.01	1.05±0.03	0.18±0.01	n.t.	4.18±0.28
Gelidium pusillum (Stackhouse) Le Jolis	Port Lonsdale, VIC	2.06±0.24	0.04±0.01	0.92±0.59	0.23±0.03	n.t.	3.25±0.80
Hymenema curdieana (Harvey) Kylin	Warrnambool, VIC	n.t.	n.t.	0.01±0.00	n.t.	n.t.	0.01±0.00
Hymenocladia chondricola (Sonder) Lewis	Port Lonsdale, VIC	n.t.	n.t.	n.t.	n.t.	n.t.	n.t.
Hypnea episcopalis Hooker et Harvey	Warrnambool, VIC	n.t.	n.t.	n.t.	n.t.	n.t.	n.t.
Jania micrarthrodia J.V.Lamouroux	Port Lonsdale, VIC	0.98±0.07	0.01±0.00	1.15±0.14	0.06±0.01	n.t.	2.20±0.08
Jania sp.	Sorrento, VIC	n.t.	n.t.	n.t.	n.t.	n.t.	n.t.
Laurencia botryoides (Turner) Gaillon	Sorrento, VIC	0.40±0.12	0.01±0.00	0.28±0.06	0.04±0.01	0.31±0.09	1.04±0.27
Laurencia elata (C. Agardh) Harvey	Port Lonsdale, VIC	1.58±0.26	0.04±0.01	1.70±0.22	0.25±0.05	0.38±0.09	3.95±0.38
Laurencia filiformis (C.Agardh) Montagne	Port Lonsdale, VIC	0.34±0.05	0.01±0.00	0.64±0.03	0.05±0.01	n.t.	1.04±0.02
Laurencia rigida J. Agardh	Batemans Bay, NSW	0.07±0.01	1.52±0.45	0.19±0.04	0.07±0.02	0.05±0.02	1.90±0.52
Laurencia tumida Saito et Womersley	Port Lonsdale, VIC	0.54±0.22	0.01±0.00	0.63±0.22	0.04±0.01	n.t.	1.23±0.45
Metagoniolithon stelliferum (Lamarck) Weber-van Bosse	Sorrento, VIC	0.68±0.08	0.02±0.01	n.t.	0.03±0.01	n.t.	0.70±0.08
Nizymenia australis Sonder	Port Lonsdale, VIC	n.t.	n.t.	n.t.	n.t.	n.t.	n.t.
Nizymenia conferta (Sonder) Chiovitti, Saunders & Kraft	Port Lonsdale, VIC	n.t.	n.t.	n.t.	n.t.	n.t.	n.t.
Phacelocarpus alatus Harvey	Port Lonsdale, VIC	n.t.	n.t.	n.t.	n.t.	n.t.	n.t.
Plocamium angustum (J.Agardh) Hooker et Harvey	Port Lonsdale, VIC	0.25±0.11	0.01±0.00	0.36±0.22	0.02±0.01	n.t.	0.63±0.21
Plocamium dilatatum J.Agardh	Warrnambool, VIC	2.21±0.40	0.04±0.01	0.76±0.30	0.14±0.06	n.t.	3.15±072
Plocamium mertensii (Greville) Harvey	Port Lonsdale, VIC	0.70±0.08	0.02±0.01	0.43±0.03	0.11±0.01	n.t.	1.26±0.11
Porphyra columbina Montagne	Batemans Bay, NSW	0.92±0.13	1.88±0.35	0.16±0.05	n.t.	n.t.	2.95±0.52
Pterocladia capillacea (S.G.Gmelin) Santelices & Hommersand	Batemans Bay, NSW	2.40±0.40	0.04±0.01	0.05±00.01	0.04±00.02	n.t.	2.52±0.41
Rhodymenia australis (Sonder) Harvey	Warrnambool, VIC	0.08±0.05	n.t.	0.05±0.03	0.01±0.00	n.t.	0.13±0.05
Wollastoniella sp.	Warrnambool, VIC	n.t.	n.t.	n.t.	n.t.	n.t.	n.t.
Wrangelia velutina (Sonder) Harvey	Warrnambool, VIC	0.03±0.01	0.01±0.00	n.t.	n.t.	n.t.	0.04±0.01

DISCUSSION

This study provides the first comprehensive survey of the qualitative and quantitative occurrence of MAAs in red macroalgae from temperate Australia. In contrast to brown and green macroalgae, UV-absorbing substances have been widely observed in many species of the Rhodophyta (Sivalingam et al. 1974; Sivalingam and Nisizawa 1990; Wood 1989; Karentz et al. 1991; Maegawa et al. 1993; Molina and Montecino 1996; Karsten et al. 1998 a,b). In the present study, the MAA concentrations measured in typical intertidal algae such as *Bangia atropurpurea* and *Capreolia implexa* are approximately >20-fold higher compared to sublittoral species such as *Ballia callitrichia*. This is in good agreement with earlier reports on Rhodophyta from Arctic to warm-temperate localities (Maegawa et al. 1993; Karsten et al. 1998a) which indicate that species from deeper water exhibit only trace amounts or even lack these compounds.

The red algae can tolerate a wider range of radiation levels than any other group of macroalgae. The deepest known plant is a coralline-like species found at 268 m off the Bahamas that grows at < 0.1 µmol photons m^{-2} s^{-1} (Littler et al. 1985). Other members of the group well reproduce and survive in the upper intertidal zone, often fully exposed to bright sunlight at >2200 µmol photons m^{-2} s^{-1} (Pedroche et al. 1995). Between these extremes the radiation quality and quantity reaching different species in different depths is highly variable due to the inherent optical properties of the water column, sun angle, latitude, season and weather conditions. However, sublittoral red algae are adapted to the generally low under-water radiation climate and hence are characterised as 'shade-plants' (Raven et al. 1979; Lüning 1990). These species usually exhibit a lower photosynthetic capacity and rate of dark respiration than 'sun-plants', as well as optimum growth at low photon flux densities. Moreover, photosynthesis of macroalgae from deeper waters was shown to be particularly sensitive to UV radiation (Bischof et al. 1998). Since sublittoral plants are generally never exposed to high irradiances including UV, at least not for long periods, there is no physiological need to synthesise and accumulate metabolically expensive MAAs as indicated in the data presented. This in turn would save energy to better support other essential pathways such as, for example, light-harvesting phycobilisomes.

It had been recently reported from Malaga in southern Spain (36.6°N - similar latitude as the locations in this study) that the depth distribution of brown macroalgae on the shore is controlled by the incident UV-radiation due to the species-specific sensitivity of spores against this short wavelengths (spores from shallow water species are more resistant than spores from species collected at greater depths). This means that one specific developmental stage of the life history is the main target of UV-radiation and this may affect zonation (Wiencke at al. 2000).

Compared to sublittoral red algae, intertidal species are known to contain high contents of MAAs (Maegawa et al. 1993; Karsten et al. 1998a), which is in good agreement with the results shown. While most plants growing in this regularly exposed habitat are able to flexibly synthesise and accumulate these compounds in response to the respective radiation climate, some taxa such as *Bangia atropurpurea* exhibit always a high steady-state concentration. In this particular species cells seem to be loaded-up with the photoprotective substances, which is consistent with the typical occurrence very high on the shore.

Besides the depth zonation, the biogeographic distribution of macroalgae seems to be another important factor controlling the MAA concentrations, since species from lower, high-solar latitudes always exhibit more MAAs than species from higher, low-solar latitudes (Karsten et al. 1998a). These observations indicate that the higher the natural solar UV-radiation of the respective habitat the more MAAs are formed and accumulated in these plants.

MAAs are one of nature's sunscreens, with 19 structurally distinct compounds so far identified in marine organisms (Dunlap and Shick 1998). Although MAA levels in

macroalgae show a decline in concentration with increasing growth depth and are in general positively correlated with natural doses of UV-radiation (Karsten et al. 1998b), experimental evidence for the role of MAAs as UV-protectants in these plants is still circumstantial. Nevertheless, the presence of increasing MAA contents in the red alga *Devaleraea ramentacea* with decreasing depth strongly correlated with a more insensitive photosynthetic capacity under UV exposure (Karsten et al. 1999). Photosynthetic experiments on the unicellular microalgae *Gymnodinium sanguineum* proved that MAAs indeed act as spectrally specific UV-sunscreens (Neale et al. 1998). In marine invertebrates the function of MAAs as intracellular photon screening agents has been inferred from UV-induced delays in the first division of sea urchin embryos having low concentrations of MAAs compared to embryos with high MAA contents (Adams and Shick 1996). In another study, Dionisio-Sese et al. (1997) showed that the presence of MAAs in the surface tunic of the colonial ascidian *Lissoclinum patella* protect its photosynthetic symbiont, *Prochloron* sp., from UV-induced photodamage. Moreover, Ishikura et al. (1997) measured maximum MAA concentrations in the outermost surface layer of the siphonal mantle of the giant clam *Tridacna crocea*. The occurrence of MAAs in the animal tissue prevented an inhibition of photosynthesis of its zooxanthellae *Symbiodinium* sp., which outside the protecting animal tissue responded very sensitively to UV radiation. These authors calculated that the sunscreen capacity of the measured MAAs were sufficient to absorb 87% of 310-nm radiation and 90% of 320-nm radiation before reaching 0.2 mm depth in the siphonal mantle. All recent publications on marine algae and invertebrates strongly support the photobiological function of MAAs as a cellular defenCe system against the harmful effects of UV-radiation (Dunlap and Shick 1998).

Therefore it is concluded that the physiological capability of intertidal red algae to synthesise and accumulate high MAA concentrations plays a vital role as biochemical adaptation ensuring survival under the environmental extremes in the habitat.

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