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Mycosporine-like amino acids in mangrove-associated red algae of the Maldives: a chemical and environmental baseline for the central Indian Ocean

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Abstract

Mycosporine-like amino acids (MAAs) are small organic UV-absorbing compounds that protect algae against harmful solar radiation. While these molecules are known to strongly reflect the ecology of the algae that produce them, information of their occurrence in mangrove-associated species from the central Indian Ocean remains undocumented. This is particularly relevant in the Maldives, where evidence shows extreme climate events already caused a substantial mangrove dieback, resulting in increased local irradiance levels due to canopy loss. This study provides the first survey of MAA diversity and irradiance conditions for macroalgae in Maldivian mangrove habitats, sampled across 15 islands and 8 atolls. Photosynthetically active radiation, UV-A, and UV-B levels were measured under the mangrove canopy and in adjacent full sun. Sun-exposed positions received $\sim 5\times$ more PAR than shaded ones. Specimens were identified morphologically to species or genus level. Four MAAs (porphyra-334, palythine, shinorine, and asterina-330) were identified and quantified by HPLC-DAD across 28 samples, with total MAA contents ranging from 0.23– 6.66 mg g⁻¹ DW, with the highest concentrations detected in the red algae *Wilsonosiphonia fujiae*, *Bostrychia tenella* and *B. binderi*. The former represents the first MAA record for this species. Ten detected HPLC peaks could not be matched to available standards and are reported by their absorption maxima and retention time. *Bostrychia tenella* showed the most diverse unidentified peak profile. These findings establish a chemical baseline for Maldivian mangrove algae relevant to future conservation and restoration efforts as these habitats face increasing climate pressure, including the loss of sun-protective canopy.

Keywords:

MAA; Rhodophyta; Indian Ocean; mangrove-algal community

47 **Introduction**

48 The effects of increased levels of UV radiation (UVR) reaching the Earth's surface have
49 become an important health and ecological concern (Xie et al. 2023; Orfanoudaki et al.
50 2019). Within aquatic environments, UVR strongly affects organisms that inhabit shallow
51 waters, such as seaweeds (Karsten et al. 2007). Solar UV-B penetrates the upper layers of the
52 water impairing photosynthesis, damaging DNA, proteins, and thylakoid membranes, and
53 causing oxidative stress in phytoplankton and macroalgae if experienced at levels above
54 species-specific thresholds (Karsten, 2008; Vincent and Roy 1993). Algae have adaptive
55 mechanisms to withstand harmful effects of UV-A (315-400 nm) and UV-B (280-315 nm),
56 like the dissipation of excess energy as heat (Müller et al. 2001), the development of anti-
57 oxidative systems (Aguilera et al. 2002), and the accumulation of primary and secondary
58 metabolites, such as mycosporine-like amino acids (MAAs) (Karsten 2008). These molecules
59 are composed of a cyclohexenone or cyclohexenimine chromophore conjugated with the
60 nitrogen constituent of an amino acid or its imino alcohol (Sinha et al. 2007) and
61 characterised by their small molecular weight, high solubility, and polarity (Wada et al.
62 2015). They are among the strongest UV-absorbing natural products with absorption maxima
63 between 268–362 nm and very high absorbance coefficients, depending on their chemical
64 structure (de la Coba et al. 2019). MAAs increase UV-absorbing capacity and hence UV-
65 tolerance of the organisms that produce them and have interesting pharmaceutical
66 (Punfchakara et al. 2023) and cosmeceutical (Vega et al. 2021) applications.

67 Typically, the Rhodophyta are well known to accumulate the highest MAA
68 concentrations per dry weight of all the algal phyla and to contain the greatest variety among
69 different algal groups, with shinorine, porphyra-334, palythine, asterina-330, mycosporine-
70 glycine, usujirene, palythinol and palythene being the most abundant representatives (Karsten
71 et al. 1998). Green algae (i.e., Chlorophyta and Streptophyta) on the other hand, comprise a

generally lower number of species containing MAAs, although some aeroterrestrial species within the genera *Prasiola* and *Klebsormidium* exhibit comparable or even higher concentrations of specific MAAs (prasiolin and klebsormidin A and B, respectively) compared to Rhodophyta (Kitzing et al. 2014; Hartmann et al. 2015). Phaeophyceae typically do not contain MAAs or exhibit only trace amounts which might derive from epiphytic red algae (Orfanoudaki et al. 2019a) and, potentially, diatoms (Wang et al., 2023); cyanobacteria have also been reported to produce a high variety of MAAs, many of them remaining chemically uncharacterised (Carreto and Carignan 2011).

Several studies revealed geographic, seasonal and bathymetric trends showing that red algae from tropical zones accumulate higher amounts of MAAs than those in temperate regions, and that their concentrations increase during summer and decrease with water depth (Briani et al. 2018; Huovinen et al. 2004; Karsten et al. 1998, Moreira et al. 2024). All these facts indicate the important role of MAAs as photoprotective agents (Ayoub et al. 2012; Karsten et al. 2006). Monitoring the MAA pattern is therefore an important task, since it can be related to ecological and chemosystematic research (Orfanoudaki et al. 2019a) as well as provide important information to predict how the organisms might respond to change in their habitats.

In mangrove habitats, systems particularly vulnerable to increased irradiance due to canopy loss (Stewart et al. 2021), MAAs are well reported in genera of Ceramiales (e.g., *Bostrychia*, *Caloglossa*) typically found in association with mangrove roots (Karsten et al. 2000, Urrea-Victoria et al. 2023, 2025). Common compounds isolated from these include mycosporine-glycine, shinorine, porphyra-334, asterina-330, and palythanol (Karsten et al. 2000). Additionally, *Catenella repens* (Caulacanthaceae, Gigartinales) produces two unique, novel UV-absorbing compounds that absorb at 324 and 320 nm (Hartmann et al. 2015).

While MAAs from tropical habitats are reported, many equatorial regions are still poorly represented (Orfanoudaki et al. 2019a), and no information is available from the central Indian Ocean. Maldivian mangroves are under increasing pressure from climate change (Dhunya et al. 2017), with a recent survey reporting a 25% dieback of mangrove trees across the country since 2020 (Carruthers et al. 2024). While at the regional scale there is some evidence of a “dimmed” solar radiation over the Indian Ocean due to increased atmospheric water vapor (Allan et al. 2025), the reduction in canopy cover due to tree loss would result in a drastic local increase in the irradiance levels. For example, Yokoya et al. (1999) measured incident photosynthetically active radiation (PAR) above the canopy of mangrove trees in Brazil and below the canopy at the height of algae growing epiphytically on mangrove tree prop roots. These authors reported that the amount of light penetrating the canopy, from the densest to the sparsest canopy cover extent, was between 5% and 17%, respectively, of the irradiance measured under direct sunlight. Canopy loss could therefore represent a potential threat to photosynthetic organisms due to the already mentioned negative effects that accompany increase in UV radiation. This is particularly relevant to organisms that live on mangrove tree roots, such as epiphytic algae, that are often exposed to strong tidal flux resulting in their emersion for several hours during the day, thus being more exposed to UV radiation (Karsten et al. 2000).

This study provides the first survey of the MAA profiles of macroalgae found in mangrove habitats in the Maldives, coupled with *in situ* measurements of the irradiance levels in which they grow, in order to establish baseline information of what constitutes their chemical defenses and the environmental context in which they currently operate. This information is useful to guide potential restoration and conservation efforts.

Materials and methods

Study sites and irradiance

The survey was conducted in 15 islands across 4 northern, 3 central, and 1 southern atolls in mangrove habitats of the Maldives (Fig. 1). Sites were selected based on a recent review on the mangrove trees distribution in the country (Cerri et al. 2024). Coordinates and habitat details are reported in Table S1.

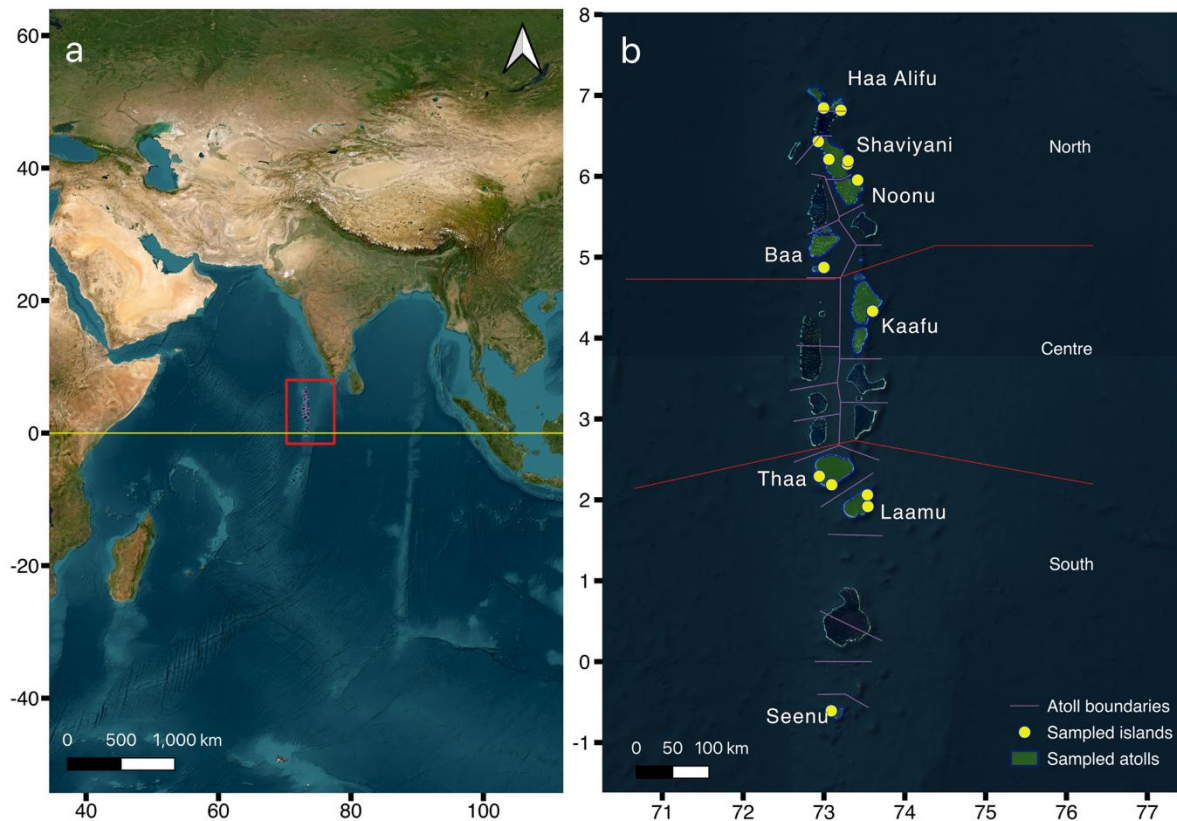


Fig. 1. (a) Location of the Maldives in the Indian Ocean. (b) sampling locations in the Maldives. The Maldivian atolls have been divided into northern, central and southern. Latitudes and longitudes shown on axes. Map generated using QGIS 3.36.3 (QGIS Development Team, 2026).

Irradiance was measured at each site using the multifunction handheld datalogger HD31 (Delta Ohm, Caselle Di Selvazzano, Italy) with probes to measure photosynthetically active radiation (PAR) (LP471PAR), UV-A (LP471UVA), and UV-B (LP471UVB). Photosynthetically active radiation ($\mu\text{mol photons m}^{-2} \text{ s}^{-1}$), UV-A and UV-B (both $\mu\text{W cm}^{-2}$)

were recorded simultaneously with repeated readings taken over a few seconds at each position. Measurements were taken close to the algal biomass under the mangrove tree canopy, and in the full sun for comparison. The “shade” vs “full sun” measurements were always taken within a few minutes from each other.

Sample collection and identification

Macroalgal material was collected both from mangrove tree roots and from surrounding substrate (e.g., dead tree trunks, seagrass, sediment), placed in Ziploc bags, and transported back to the base island in a cooler.

Specimens were first cleaned from epiphytes, then observed and photographed under a compound microscope (Leica, model DM 500, Wetzlar, Germany) equipped with a camera (Leica Flexacam, model i5, Wetzlar, Germany). The samples were examined for reproductive structures and other distinctive morphological traits. In some cases, a razor blade was used to obtain cross-sections of thalloid specimens.

Samples were identified morphologically to the lowest taxonomic level by R.N. and G.C.Z, according to standard identification keys that also include information about geographic distribution of taxa (AlgaeBase, Guiry and Guiry 2014). and comparing our findings with currently available information from the region (e.g., Nicolai et al. 2025; Boo et al. 2020; Silva et al. 1996). After the microscopic examination, each sample (~5 g FW) was dried in silica gel for High-Performance Liquid Chromatography (HP-LC) analysis.

MAA analysis

The dried algal samples were powdered using a mortar and pestle. Algal biomass of each sample was used for mycosporine-like amino acid (MAA) analyses by HP-LC (Karsten et al. 2000). MAAs were extracted from the powdered algal samples (~10 mg of dry weight – DW, n=3) in 1 mL of aqueous 25% methanol (v/v, HPLC grade) in a water bath (45°C) for 3

hours. During the extraction time in the water bath, the samples were vortexed regularly to optimize extraction. Then, the samples were centrifuged at 13,000×g for 15 min and the methanolic supernatants were transferred to new microtubes, followed by evaporation to dryness in a Speed Vacuum Concentrator (RVC 2–25 CDplus, Christ, Osterode, Germany). After this, the dried pellets were re-dissolved in 1 mL of HPLC water. Aqueous homogenates were vortexed for 30 s and then centrifuged at 13,000×g for 15 min. Finally, the aqueous supernatants were transferred to HPLC vials after passing through a 0.45 µm filter (Whatman, Dassel, Germany) prior to injection onto the HPLC column. MAAs in the samples were analysed qualitatively and quantitatively using a 1220 Infinity II HPLC system (Agilent Technologies, Waldbronn, Germany) with a diode array detector (DAD: 330 nm, range: 240–400 nm). A Phenomenex Synergie 4m fusion RP column (C18, 4 mm, 250 × 3mm, Phenomenex, Aschaffenburg, Germany) protected by a guard cartridge (RP-18 4 × 3 mm I.D., Phenomenex) was used to identify MAAs. During measurements the mobile phase (eluent) was 2.5% methanol (v/v) plus 0.1% acetic acid (v/v) with a flow rate of 0.5 mL min⁻¹, 150 bar pressure, column temperature at 30 °C, and 10 µL as the injection volume. The sample chromatograms were compared with those from biological standards of palythine, asterina-330, shinorine, and porphyra-334 to identify MAAs by retention time (RT) and absorbance spectrum (λ_{max}). The area under the integrated peaks of the samples and reference concentrations of MAAs in their biological standards were used to quantify MAAs in the macroalgae (mg g⁻¹ DW).

Samples were analysed in two separate runs, and standards were injected at the beginning, middle and end of each run to monitor retention-time stability.

Peaks whose λ_{max} differed by ≤1 nm from an available standard were assigned that MAA as a putative identification (indicated by an asterisk) and quantified using the corresponding response factor. Peaks differing by >1 nm from every standard could not be

assigned; these were designated by their λ_{max} (e.g. 324 nm), quantified only in terms of retention time and peak area, and excluded from total MAA content.

Daily and annual photon dose estimation

To place the measured shade and sun irradiance values in an ecologically meaningful context, we additionally estimated the daily and annual photon dose received by algae in each microhabitat. This calculation follows the standard concept of the Daily Light Integral (DLI), a widely used metric for characterizing cumulative photon exposure in plant and algal photobiology (Faust and Logan 2018) and in marine benthic phototrophs specifically (DiPerna et al. 2018). Since our irradiance readings represent a single, close-to-midday value at each site rather than a continuously logged diurnal cycle, we treated each mean PAR value as a representative midday peak (I_{peak}). We then modelled the diurnal course of irradiance as a half-sine function, a standard first-order approximation for converting a single peak reading into a daily total when continuous logging is unavailable. Under this model, the mean irradiance across the sunlit period is $(2/\pi) \times I_{\text{peak}}$. Daily photon dose was calculated as:

$$\text{DLI (mol photons m}^{-2} \text{ day}^{-1}) = I_{\text{peak}} \times (2/\pi) \times (S \times 3600) / 1,000,000$$

where S is the mean daily sunshine duration in hours. We used the Maldives' annual mean sunshine duration (7.6 h day⁻¹; Maldives Meteorological Service, <https://www.meteorology.gov.mv/climate>; Weather-and-Climate.com, https://weather-and-climate.com/average-monthly-hours-Sunshine,male-mv,Maldives#google_vignette) as S , since daylength itself varies negligibly at this equatorial latitude (approximately 11:55–12:24 h year-round). Most seasonal variation in received light is instead driven by cloud cover and monsoon timing rather than daylength. Annual photon dose was estimated by multiplying the daily estimate by 365. This calculation is a first-order approximation derived from spot measurements rather than continuous field logging, intended to indicate the scale of

207 difference between shaded and full-sun conditions rather than to provide a precise annual
208 total.

209 **Statistics**

210 Shade versus sun comparisons for PAR, UV-A and UV-B were tested using site-level means
211 (one paired shade value and one paired sun value for each of the eight sampling sites). For
212 each variable, the paired differences (sun – shade) were checked for normality (Shapiro–Wilk
213 test); a paired t-test was used where this assumption was met, and a paired Wilcoxon signed-
214 rank test was used otherwise.

215 **Results**

216 **Environmental data**

217 Habitats varied from sandy embayments adjacent to muddy areas surrounding the mangrove
218 (Fig. 2a, b), to semi-enclosed lagoons full of tannins (Fig. 2c), coastal habitats with extensive
219 seagrass meadows (Fig. 2d), and completely exposed mangrove trees with scarce canopy
220 cover (Fig. 2e).

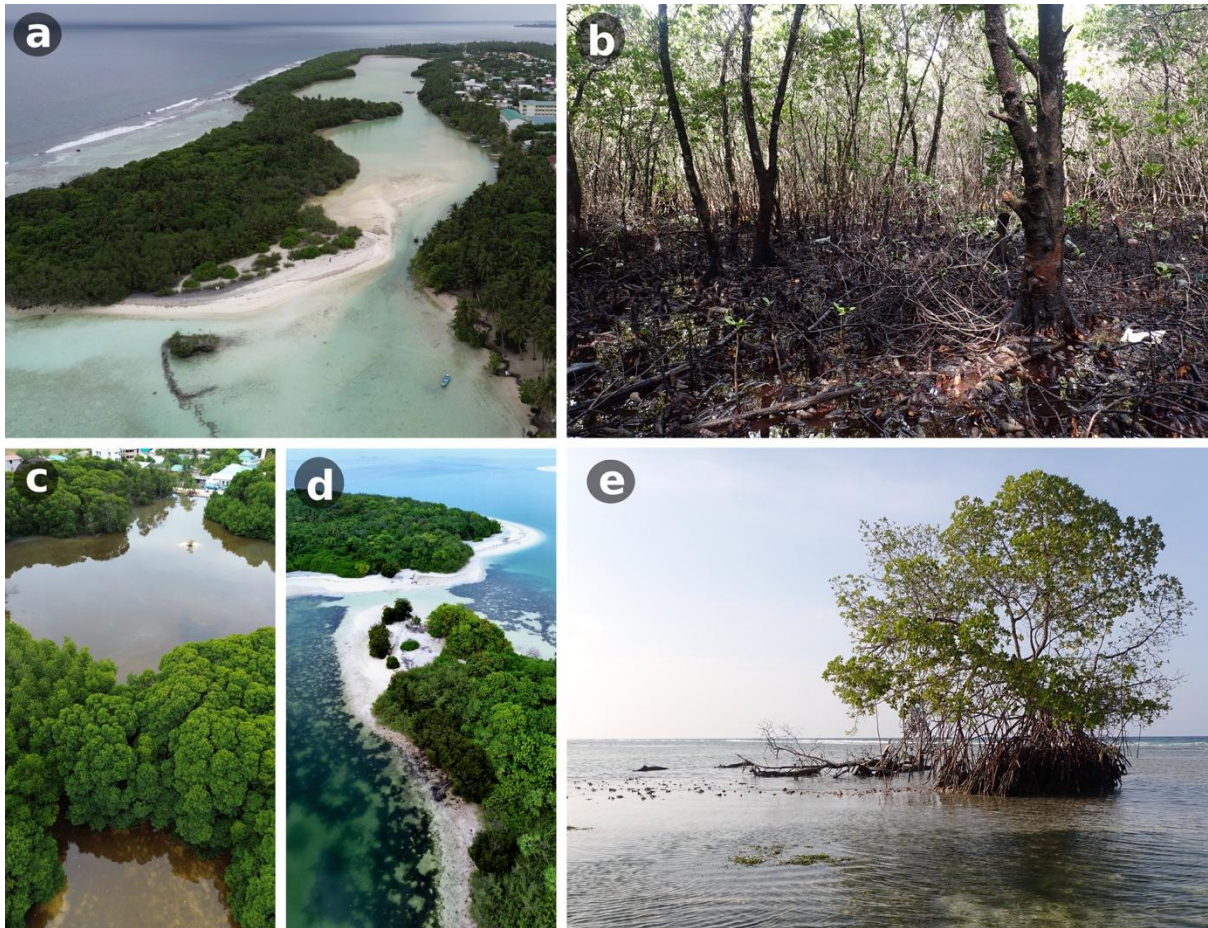
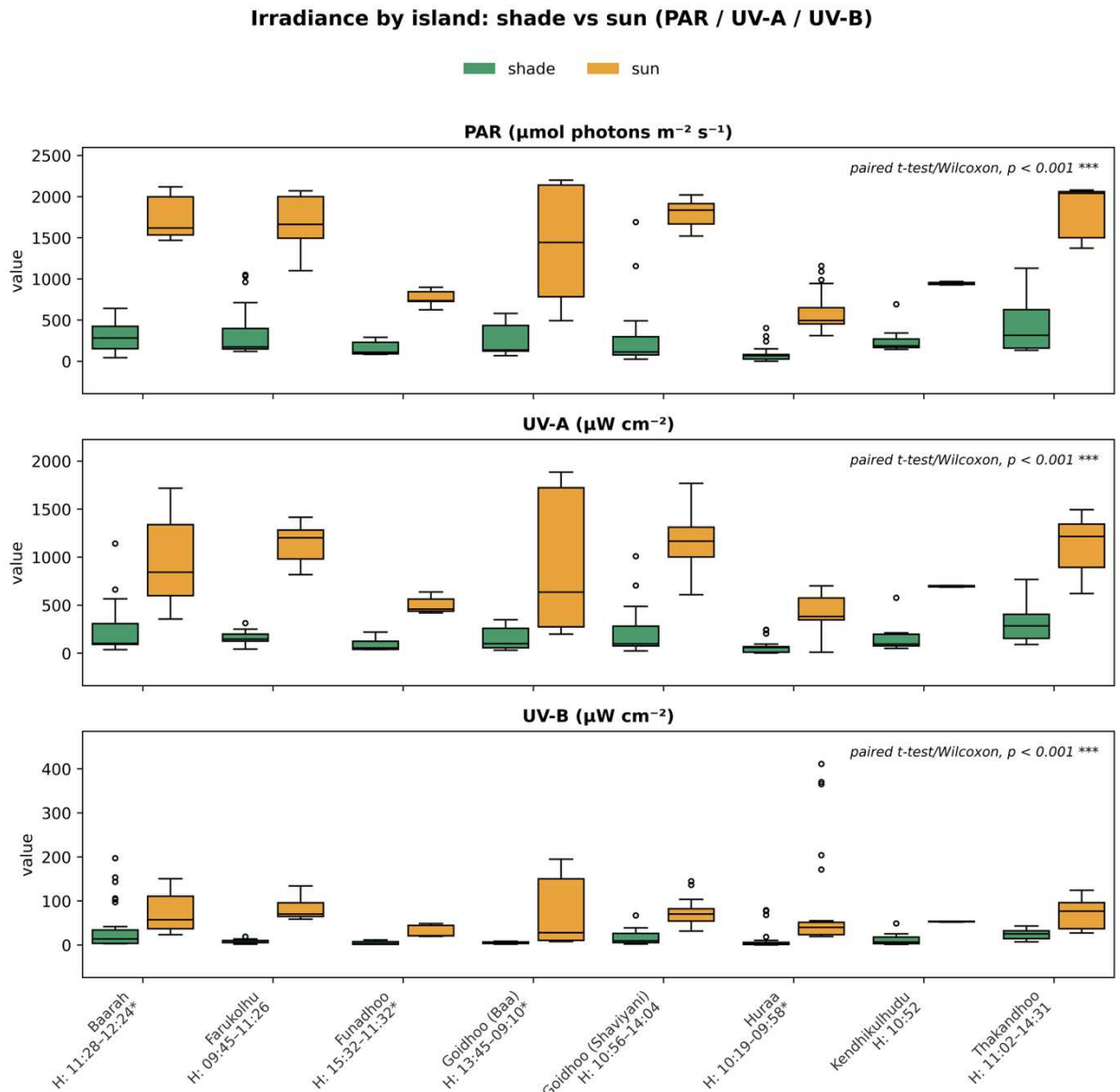


Fig. 2. Habitat overview: (a) sandy embayment and (b) muddy, damp substrate with *Rhizophora mucronata* and *B. cylindrica* mangrove trees in Funadhoo, Shaviyani. (c) muddy, connected to the port (Huraa, Kaafu) (d) embayment with sandy substrate and seagrass meadows; (e) coastal, completely exposed mangrove, algae were found on mangrove roots and on surrounding rocky substrate (Goidhoo, Baa).

Sun-exposed positions received approximately 5-fold more PAR than adjacent shaded positions depending on the island, with comparable enrichment in UV-A and UV-B (Fig. 3). The lower values measured in Kaafu Huraa reflect overcast days. Islands are shown separately and are not pooled; the two Goidhoo sites are distinct islands in two atolls (Baa and Shaviyani).



H = start time of the first reading of each measurement set; * = sets spread over more than one day

233

234 Fig. 3. Irradiance (PAR: $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$; UVA and UVB: both $\mu\text{W cm}^{-2}$) in shaded

235 (green) versus sun-exposed (orange) microhabitats at the eight islands where MAA-

236 containing algae were sampled. Boxes show the median and interquartile range, whiskers

237 extend to $1.5 \times \text{IQR}$, and points denote values beyond that range. Beneath each island name,

238 H gives the local time of the first reading shown as the range from the earliest to the latest; *

239 indicates that these sets were distributed over more than one day (all within the same

240 sampling period). Because measurements were not all taken at solar noon, absolute values

241 partly reflect time of day; shaded and sun-exposed positions at a given island were

nevertheless measured within minutes of each other, so the within-island contrast is unaffected. Islands are shown separately and are not pooled; the two Goidhoo sites (Baa and Shaviyani atolls) are distinct islands.

Mean PAR was 267.2 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$ in shade vs 1339.9 in full sun; mean UV-A was 171.7 vs 858.6 $\mu\text{W cm}^{-2}$; and mean UV-B was 13.8 vs 66.5 $\mu\text{W cm}^{-2}$ (shade vs sun respectively; $n = 8$ sites shared between the environmental survey and algal sampling). Sun-exposed positions were significantly higher for all three variables (paired t-test on site-level means; PAR, UV-A and UV-B all $p < 0.001$).

Using these mean PAR values, estimated daily light integrals in shaded positions received 4.7 $\text{mol photons m}^{-2} \text{ day}^{-1}$ ($\sim 1700 \text{ mol photons m}^{-2} \text{ yr}^{-1}$), compared with 23.3 $\text{mol photons m}^{-2} \text{ day}^{-1}$ ($\sim 8500 \text{ mol photons m}^{-2} \text{ yr}^{-1}$) in full sun, roughly a five-fold difference in estimated annual photon dose.

Algal taxonomic diversity

The most frequently observed taxa were two species in the genus *Bostrychia*, *B. tenella* ($n=12$) and *B. binderi* ($n=3$), and the species *Wilsonosiphonia fujiae* ($n=8$), all growing directly under the tree canopy on mangrove roots. Samples in the genus *Bostrychia* were distinguished to species level on the basis that, while both are characterised by the presence of a corticated main axis (Fig. 4a, b), *B. tenella* has multiple discoid plastids and long, monosiphonous laterals (Fig. 4c) that give the thallus a feathery appearance (Fig. 4d), while *B. binderi* has shorter, spine-like laterals (Fig. 4e, f) (Zuccarello et al. 2015). Both species were most frequently found on the knee roots of the mangrove *Bruguiera cylindrica* and prop roots of *Rhizophora mucronata* (Fig. 4g, h), but they were also observed to grow between crevices of rocks and dead trunks of other tree species (Fig. 4i).

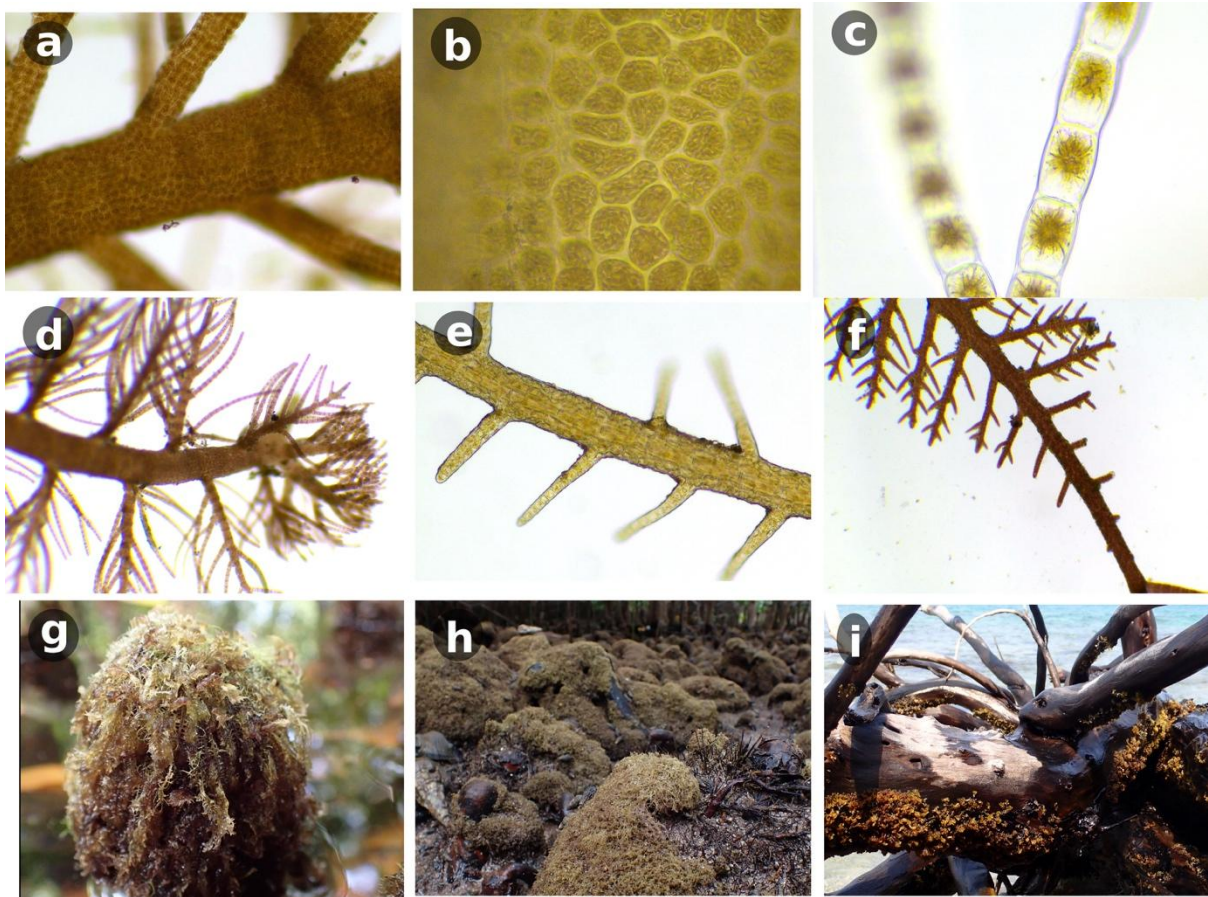


Fig. 4 Morphology and growth habits of *Bostrychia tenella* and *B. binderi*. (a, b) corticated main axis. (c) long monosiphonous laterals with multiple discoid plastids and (d) abundant, feathery laterals typical of *B. tenella* in contrast to e, f) short and sparse spine-like laterals of *B. binderi* (f). (g, h) photos of *B. tenella* and (i) *B. binderi* growing on mangrove roots.

Wilsonosiphonia fujiae was identified by the 14 pericentral cells around the axial cell (Fig. 5a), branched multicellular rhizoids (Fig. 5b), and numerous branched trichoblasts at the apex of some axes (Fig. 5c) (Bustamante et al. 2017). This identification was further supported by the already reported molecular confirmation of the species in the Maldives by Boo et al. (2020). Similar to *Bostrychia*, this species was found growing as turf on dead trees and rocks (Fig. 5d, e), but the highest abundance (personal observation) was found when it was recorded growing as an epiphyte on mangrove roots (Fig. 5f).

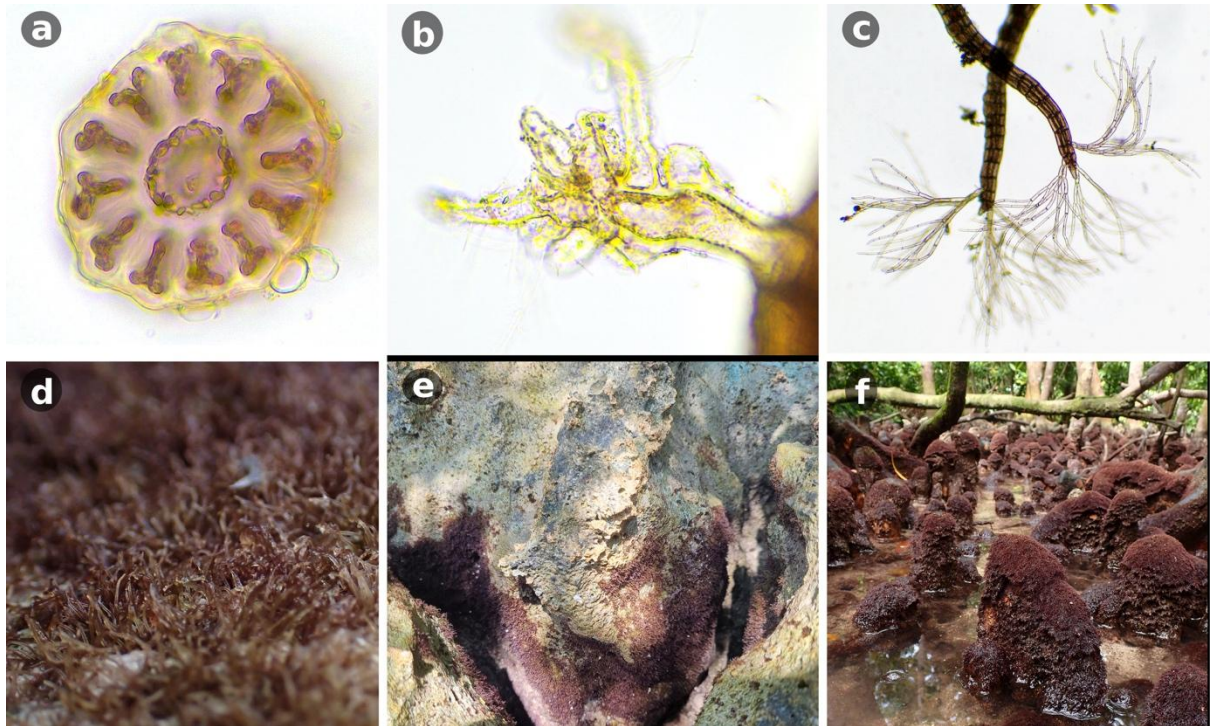
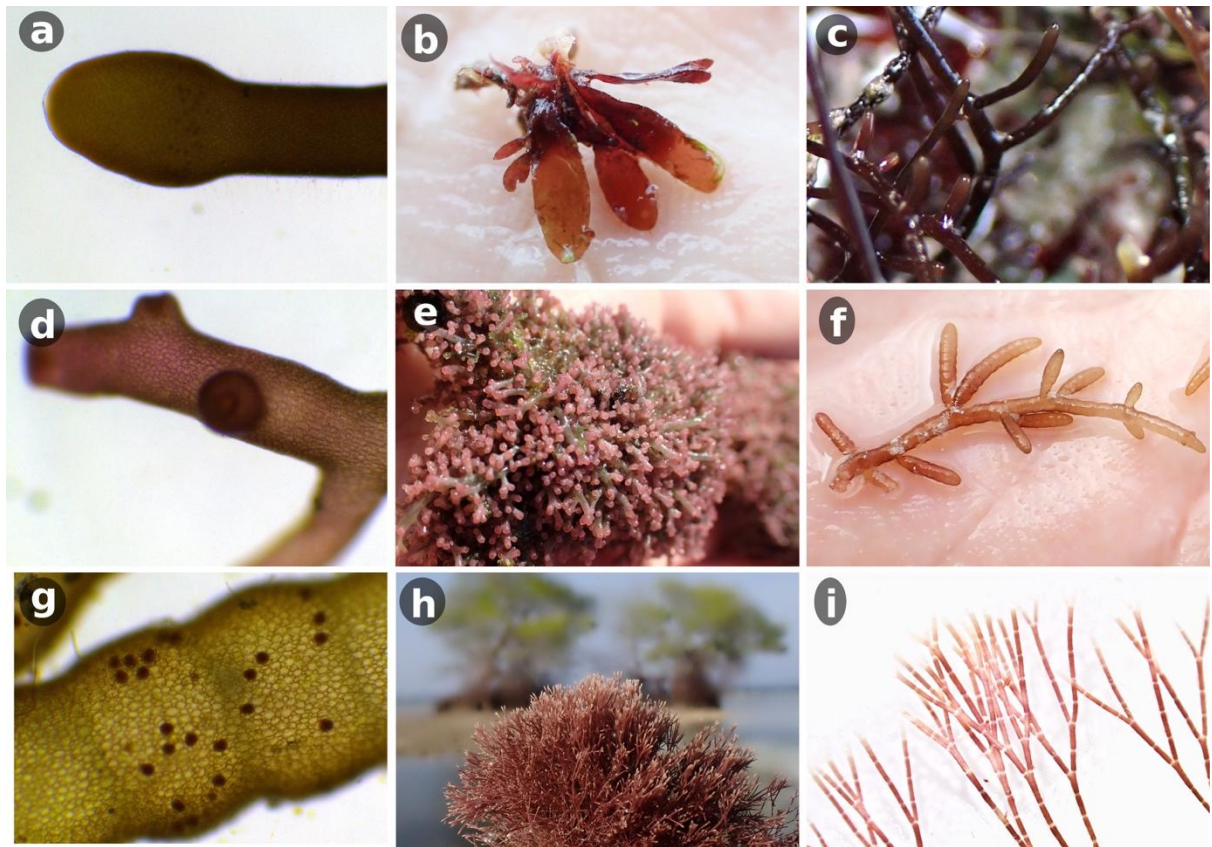


Fig. 5 Morphology and growth habit of *Wilsonosiphonia fujiae*. (a) Transverse section with 14 pericentral cells around the axial cell. (b) branched multicellular rhizoid. (c) Numerous branched trichoblasts at the apex of some axes. (d) growth habit of *W. fujiae*. (e, f) *W. fujiae* growing in rock crevices (e) and *Bruguiera cylindrica* knee roots (f). Scale bars = 0.1 mm.

Only incidental collections of the other taxa occurred. Of these, *Pterocladia* *caerulescens* (Gelidiaceae) was identified by percurrent, pinnately/distichously branched axes (Fig. 6a, b), and *Gelidiella fanii* was identified as growing stolon-like, creeping axes, with cylindrical to compressed main axis bearing slender branchlets (Fig. 6c). Some of the other samples were only identified to the genus-level, distinguished by morphological features such as: corticated axis compressed with a polysiphonous construction and distinctive refractile 'corps en cerise' in the cortical cells for *Laurencia* sp. (Rhodomelaceae) (Fig. 6d, e); hollow, constricted terete axes with internal transverse diaphragms dividing the cavity into chambers (Fig. 6f) and hemispherical tetrasporangial conceptacles (200-450 μ m diameter) scattered over the surface of *Champia* sp. (Champiaceae) (Fig. 6g); densely, mostly dichotomously

293 branched calcified tufts with an architecture of alternating calcified segments (intergenicula)
 294 and flexible, uncalcified joints (genicula) of *Jania* sp. (Corallinaceae) (Fig. 6h, i). *Champia*
 295 sp., *Pterocladia* *caerulescens*, and *Gelidiella* *fanii* were observed between and underneath
 296 rocks, while *Laurencia* sp. and *Jania* sp. were found growing among seagrass meadows and
 297 in the surrounding sediment, in full sun.



298
 299 Fig. 6. Additional algal taxa collected as incidental specimens. (a, b) *Pterocladia*
 300 *caerulescens* (Gelidiaceae): (a) percurrent, terete axis apex; (b) pinnately to distichously
 301 branched thallus habit. (c) *Gelidiella* *fanii* (Gelidiellaceae): stolon-like, creeping axis, with a
 302 cylindrical to compressed main axis bearing slender branchlets. (d, e) *Laurencia* sp.
 303 (Rhodomelaceae): (d) compressed, corticated axis of polysiphonous construction, with a
 304 refractile 'corps en cerise' visible within cortical cells; (e) overall thallus habit. (f, g) *Champia*
 305 sp. (Champiaceae): (f) hollow, constricted terete axis, with internal transverse diaphragms
 306 dividing the thallus into chambers; (g) hemispherical tetrasporangial conceptacles (200–450

307 μm diameter) scattered over the segment surface. h, i *Jania* sp. (Corallinaceae): (h) densely,
 308 mostly dichotomously branched tufted habit; (i) articulated construction, showing alternating
 309 calcified intergenicula and flexible, uncalcified genicula. Scale bars = 0.1 μm (a, d, f, g, i).

310 MAA diversity

311 Fourteen compounds were detected across the 30 samples, of which four (porphyra-334,
 312 asterina-330, palythine, shinorine) were identified and quantified against available standards.
 313 The remaining 10, comprising 24% of total individual peak occurrences across all samples,
 314 were designated only by their absorption maxima (λ_{318} , 322, 323, 324, 326, 328, 336, 358,
 315 359, 361 nm) (Table 1). Of the quantified compounds, porphyra-334 (P334) was the most
 316 frequently encountered (n=25), followed by palythine (n=22), shinorine (n=12) (SH), and
 317 asterina-330 (n=9) (AS330).

318 Table 1 Distinct unidentified ("unknown") mycosporine-like amino acid peaks, ordered by
 319 lambda-max, with the species and samples in which each was detected

λ_{max} (nm)	Mean RT (min)	n samples	Species	Sample ID(s)
318	5.20	1	<i>Bostrychia tenella</i>	HA5TB2
322	3.11	2	<i>Bostrychia tenella</i>	HA5TB3; SH13MB6
322	4.60	3	<i>Bostrychia binderi</i>	HA3BB1.1; HA3BB1.3; HA7BB1
323	3.28	1	<i>Jania</i> sp.	BGOI <i>Jania</i>
323	4.86	2	<i>Bostrychia tenella</i>	HA5TB1; SH13MB6
324	2.20	1	<i>Jania rosea</i>	AD3HUJania2
324	4.93	6	<i>Bostrychia tenella</i>	AD1HI1B_tenella; HA5TB2; SH10FB2; SH6GB_2; SH6GB1; SH9FB1.3
324	5.35	1	<i>Bostrychia tenella</i>	AD2HIBtenella
326	3.68	1	<i>Bostrychia tenella</i>	SH9FB1.3
326	5.09	2	<i>Bostrychia tenella</i>	HA5TB2; HA5TB3
328	3.59	3	<i>Bostrychia tenella</i>	AD2HIBtenella; HA5TB3; SH13MB6
328	4.32	1	<i>Bostrychia tenella</i>	HA5TB1
333	5.14	1	<i>Laurencia multiclavata</i>	SH6GLau
333	6.69	1	<i>Bostrychia tenella</i>	SH9FB1.3
336	3.72	1	<i>Bostrychia tenella</i>	SH9FB1.3
358	8.03	1	<i>Bostrychia tenella</i>	SH6GB1

λ_{max} (nm)	Mean RT (min)	n samples	Species	Sample ID(s)
359	7.86	1	<i>Bostrychia tenella</i>	HA5TB1
361	8.32	3	<i>Bostrychia tenella</i>	HA5TB1; HA5TB2; SH9FB1.3

320

321 Total MAA content varied considerably among samples of the same species (Fig. 7).

322 *Wilsonosiphonia fujiae* had the highest MAA concentration, averaging $3.80 \pm 1.95 \text{ mg g}^{-1}$

323 DW across eight samples and spanning a 4.4-fold range ($1.50\text{--}6.66 \text{ mg g}^{-1}$). *Bostrychia*

324 *tenella*, the most frequently sampled species ($n = 12$), averaged $1.49 \pm 0.75 \text{ mg g}^{-1}$ DW and

325 varied 5.8-fold ($0.52\text{--}2.99 \text{ mg g}^{-1}$), while *B. binderi* ($n = 3$) averaged $0.53 \pm 0.33 \text{ mg g}^{-1}$ DW

326 ($0.23\text{--}0.89 \text{ mg g}^{-1}$) (Table S2). Relative variability was comparable across all three

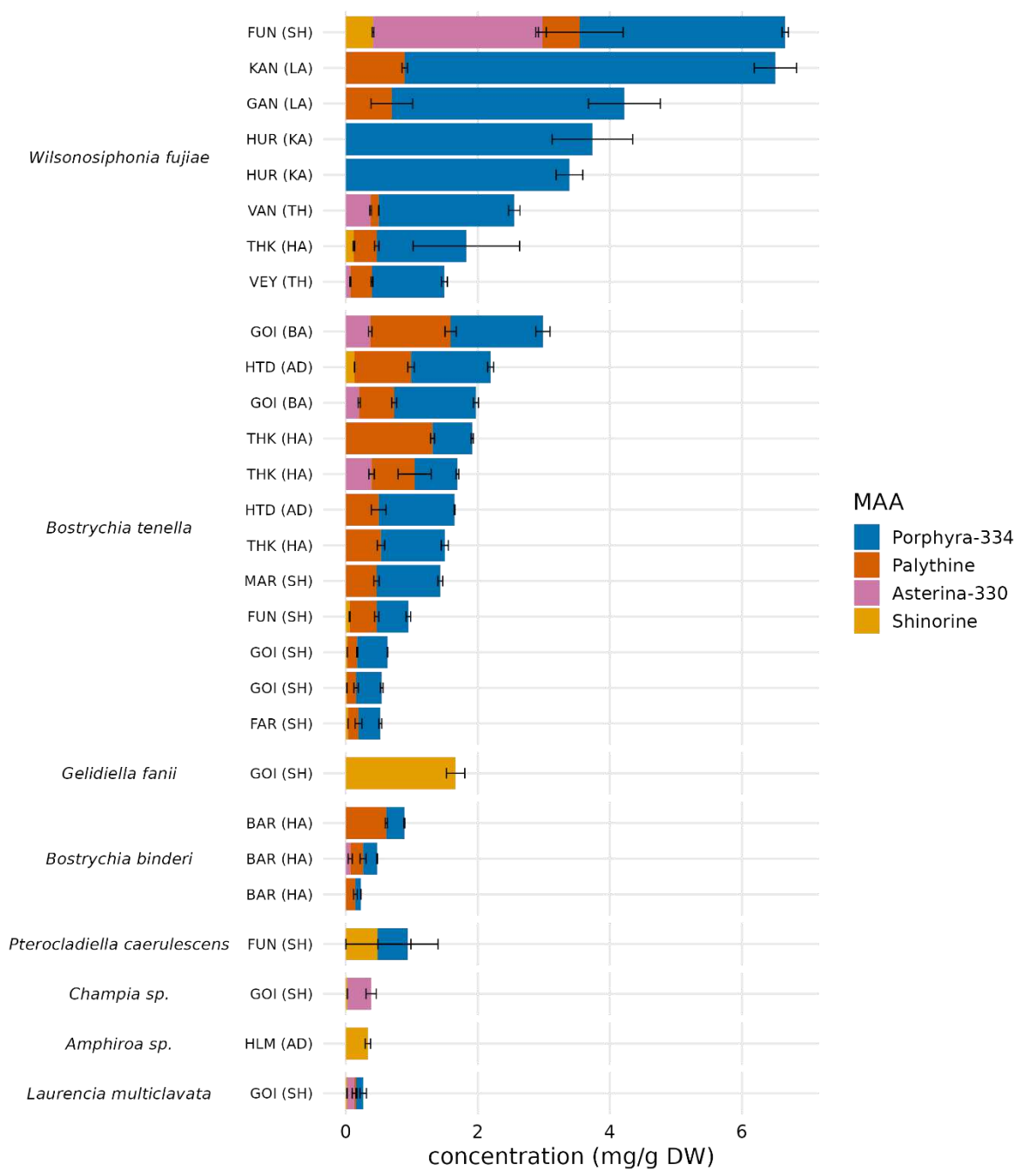
327 (coefficient of variation 49–62%), indicating that within-species differences of two- to six-

328 fold were common irrespective of the overall MAA content of the species. The remaining five

329 taxa were each represented by a single sample, so within-species variability could not be

330 assessed. In *Gelidiella fanii* and *Jania* sp., only shinorine was detected. The full per-sample

331 breakdown is provided (Table S2).



332

333 Fig. 7. MAA composition (concentration, mg g⁻¹ DW) per sample, grouped by species. Error
 334 bars show individual samples ordered by total MAA concentration within each species group;
 335 stacked segments indicate the mean concentration of each MAA (Porphyra-334, Palythine,
 336 Asterina-330, Shinorine); error bars represent ± 1 SD across replicate injections of the same
 337 sample. Site (island, atoll) is indicated below each bar.

Bostrychia tenella has the highest number of unidentified peaks, with 9 spectrally distinct compounds spanning the λ 318–328 cluster in the palythine/asterina spectral region to a late-eluting lambda-358/359/361 cluster, although not all are present across all samples and they are sometimes found only in trace amounts (Fig. 8). In the *Jania sp.* sample, only unidentified peaks were detected and were therefore not quantified.

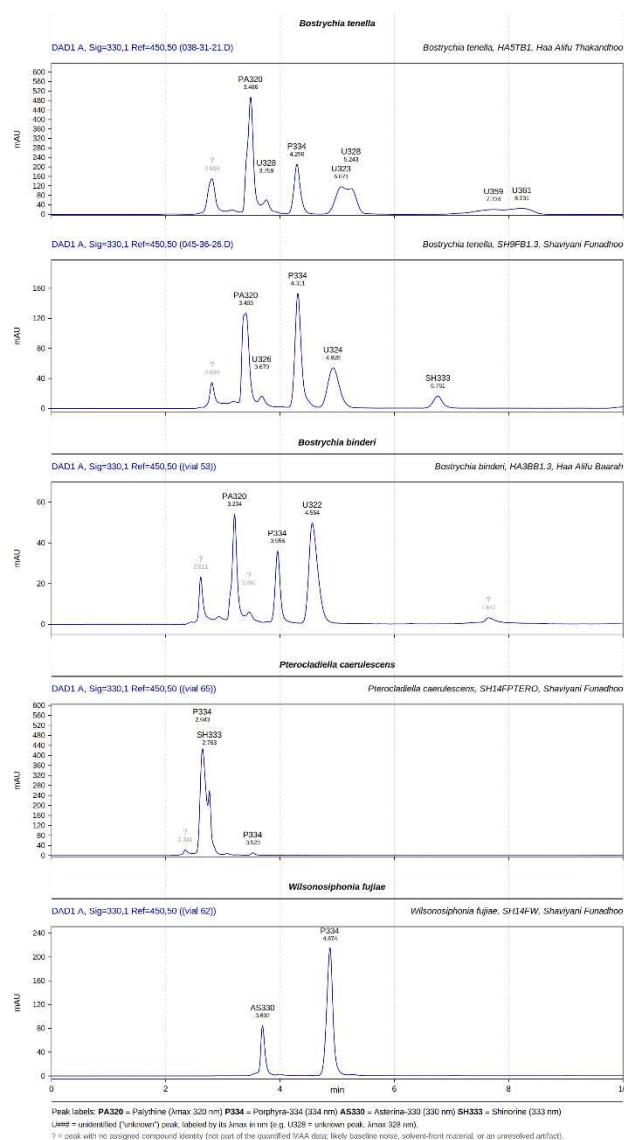


Fig. 8. Representative HPLC-DAD chromatograms (DAD1 A, Sig=330 nm) of mycosporine-like amino acids (MAAs) in mangrove-associated red algae across sites and species: *Bostrychia tenella* (HA5TB1, Haa Alifu/Thakandhoo; SH9FB1.3, Shaviyani/Funadhoo), *Bostrychia binderi* (HA3BB1.3, Haa Alifu/Baarah), *Pterocladia caerulescens*

(SH14FPTERO, Shaviyani/Funadhoo), and *Wilsonosiphonia fujiae* (SH14FW, Shaviyani/Funadhoo). All panels share the same retention-time axis (0–10 min) to allow direct comparison of peak position across samples and species; the mAU (y-axis) scale is independent per panel. Peak identities follow the abbreviation key below; unlabeled peaks (?) could not be assigned to a compound identity. This panel is included only to illustrate representative peak morphology.

Discussion

In the present study we recorded mycosporine-like amino acids (MAAs) in eight algal taxa across 15 Maldivian islands and 8 atolls, spanning the whole length of the country, with frequent observation of the Rhodomelacean algae *Bostrychia tenella*, *B. binderi*, and *Wilsonosiphonia fujiae*. This is the first study quantifying these important compounds in algae from the central Indian Ocean, since previous work from this region (India) only provided qualitative information about these molecules, but not from mangrove habitats (Ramakritinan et al. 2017, Pandey et al. 2017).

Four MAAs (porphyra-334, palythine, shinorine, and asterina-330) were quantified against available standards, with a total content ranging from 0.23-6.66 mg g⁻¹, and *W. fujiae* showing the highest concentrations in the sample collected in Huraa (Kaafu).

While taxonomic work on *Bostrychia* exists from other locations within the Indian Ocean (Lambert et al. 1987; Khin Gyi & Htun 2012; Saengkaew et al. 2016), no MAA data has previously been available from this region. The predominance of porphyra-334 in the MAA pool of *B. tenella* found in this study was also observed by Orfanoudaki et al. (2020). However, their total MAA pooled concentration was ~0.57 mg g⁻¹ DW total, comparable with the lower end detected in our study (0.52 mg g⁻¹ DW) and well below the highest amounts detected in one of our samples (2.99 mg g⁻¹). Our total concentrations for this species are comparable with field samples analysed by Karsten et al. (2000) from Indonesia (0.61 mg g⁻¹

DW), and Japan (1.62 mg g⁻¹ DW), while their Australian specimen (0.05 mg g⁻¹ DW) falls well below our lowest value.

Bostrychia tenella displayed the richest profile of unknown peaks (n=10). This is consistent with previous literature (Orfanoudaki et al. 2019b). In our samples, these unknown peaks span between the λ 318–328 cluster in the palythine/asterina spectral region, likely representing palythine-related MAAs (e.g., palythine-serine/-threonine, Carignan et al. 2009). The late-eluting λ 358–361 group is consistent (by lambda-max alone, ~357-359 nm) with the palythene/usujirene isomer pair reported in several other studies (e.g., Karsten et al. 2000; Lalegerie et al. 2024), though these results cannot be directly compared. Confirming any of these unidentified peaks would need LC-MS or the corresponding standards. However, our λ 328nm cluster matches the Borburema et al. (2022) MAA 330 (RT ~3.9 min), which followed the same protocols for extraction and HPLC analysis. In contrast, only one of the various unidentified compounds found in *B. tenella*, with λ =322, was detected in *B. binderi*.

While MAAs for the genera *Champia* and *Pterocliadiella* have been reported previously (Lee & Shiu, 2009; Orfanoudaki et al. 2019a), no data of MAAs from *Wilsonosiphonia fujiae* are found, possibly as this genus was only recently described (Bustamante et al. 2017).

Pterocliadiella caerulescens MAA concentrations from our study are similar to those measured in a study from northeastern Taiwan (Lee and Shiu 2009). The study showed that *P. capillacea* (1.4 mg g⁻¹ DW) had a higher total concentration of MAAs than *Gelidium amansii* (0.79 mg g⁻¹), with porphyra-334 being the dominant MAA in the former, and shinorine in the latter. We quantified a comparable total MAA content for *P. caerulescens* (0.94 mg g⁻¹ DW). However, the values reported from the Lee and Shiu (2009) study are from an experimental setup, where the algae were first acclimatised without UV-B exposure.

Champia novae-zelandiae is reported as one of the source species for isolating MAA standards (Orfanoudaki et al. 2019a), however specific concentrations in mg g⁻¹ DW are not

published in the literature, making our measurement (0.38 mg g⁻¹ DW) the first quantified report in this genus.

For the *Gelidiella fanii* sample, there is no direct comparison of MAA content from previous studies. Ramakritinan et al. (2017), for example, reported only qualitative information about MAAs from members of the same order Gelidiales, in *Gelidiella acerosa*, *Acantophora spicifera*, from the Gulf of Mannar (southeast coast of India), confirming the presence of a palythine-type MAA (320 nm) in these species, without quantification. Similarly, Pandey et al. (2017) only qualitatively confirmed the presence of palythine, in addition to the presence of shinorine, porphyra-334 in *Gelidium* sp. from the west coast of India.

The *Jania* sp. specimen's low MAA concentrations we measured (0.33 mg g⁻¹ DW total) are in agreement with the currently available literature (Vega et al. 2021). Our results are comparable to those reported in *Jania rubens* (0.13-0.40 mg g⁻¹ DW total) (Zwerger and Ganzera 2022), although in their study both palythine and shinorine were detected, while only shinorine was present in our specimens. Two of our *Jania* sp. samples also produced unknown peaks with λ 323 and λ 334 and RT 3.28 and 2.20, though these were detected in trace amounts (Table 1).

Finally, the measured MAA concentrations in *Laurencia multiclavata* (0.26 mg g⁻¹ DW) are well below the reported concentrations in *L. obtusa* samples from San Andrés and Providencia Islands, Colombia (1.54 mg g⁻¹ DW; Angulo-Núñez et al. 2025), which are in turn lower than samples of *L. obtusa* from the same region, reported by Urrea-Victoria et al. (2025) (>6 mg g⁻¹ DW).

The *in situ* measurements of PAR, UV-A, and UV-B clearly indicate a strong difference (4–8×) between the habitat conditions in the understory of the mangrove canopy compared to full sunlight. This highlights the magnitude of the potential impacts following

the recently observed canopy loss due to climate events affecting this region, such as the Indian Ocean Dipole Oscillation (Carruthers et al. 2024). The degree of irradiance change we measured is consistent with values reported for other tropical macroalgal habitats: full-sun PAR in this study (mean 1339.9 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$) falls within the range measured directly above intertidal macroalgae in Hawaii (mean 1415 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$; Cox & Smith, 2015), and is of the same order as the above-canopy PAR reported for Brazilian mangroves (Yokoya et al. 1999). The shaded mean we measured (267.2 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$) also closely matches shaded PAR conditions reported for Brazilian mangrove understories, where canopy attenuation reduces incident PAR to approximately 5–17% of full sun, equivalent to 170–443 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$ at their site (derived from Yokoya et al. 1999).

Translating the measured PAR values into an estimated annual photon dose, canopy loss would raise the total annual photon dose experienced by currently shade-adapted algae roughly five-fold (from ~ 1700 to $\sim 8500 \text{ mol photons m}^{-2} \text{ yr}^{-1}$). While MAA content can be upregulated in response to moderate increases in irradiance, this capacity is limited. In *Bostrychia calliptera* and *B. montagnei*, for example, MAA content was shown to gradually increase with increased photon flux, only to decline above $\sim 267\text{--}638 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$, with several compounds becoming undetectable (Borburema et al. 2022). This pattern is similar in *Pterocliadiella capillacea*, where MAA content peaked at 1.0 W m^{-2} UV-B before declining at higher radiation doses (Lee and Shiu 2009). This collapse likely reflects UV-induced impairment of the photosynthetic apparatus that underlies MAA biosynthesis (Kräbs et al. 2004). Given that even in MAA-rich species, these molecules filter at most $\sim 72\%$ of incident UV (Riegger & Robinson 1997), the ~ 5 -fold increase in irradiance measured in this survey that would result from canopy loss is unlikely to be within the adaptive range of these species.

Some of the species we encountered may not be affected at all, while others could be more sensitive. Since specimens in the genus *Bostrychia* and *Wilsonosiphonia* were found on mangrove roots, under the canopy of the trees, the loss of such shade is likely going to have an impact on these genera, while algae that grow in rocks crevices, such as *Champia* sp., *Pterocliadiella caerulea* and *Gelidiella fanii*, occur in habitats that already act as “sun shelters”. On the other hand, while *Jania* sp. was found growing in the full sun, our samples had very low MAA concentrations. A possible explanation for this can be their rich calcification, which could physically absorb and scatter UV radiation, functioning as a structural, non-chemical alternative to biochemical UV screens like MAAs (Reef et al. 2009; Vega et al. 2021).

The potential disappearance of turf-forming genera like *Bostrychia* and *Wilsonosiphonia* under increased irradiance could have cascading impacts on the fauna that depend on them, since structurally complex algal turf is known to enhance associated invertebrate biodiversity by increasing habitat complexity (Kelaher 2002). In Brazilian mangroves, for example, *Bostrychia*-dominated turf communities growing on pneumatophores support significantly greater macrofaunal abundance and diversity than bare root surfaces, with the turf's physical structure providing refuge from predation and desiccation for a range of gastropods and other invertebrates (García et al. 2016).

Overall, our findings expand the known geographic range of MAA-producing mangrove algae into the central Indian Ocean and provide a chemical and environmental baseline against which future changes can be assessed. Given their high MAA content, species such as *W. fujiae* may also warrant future attention as a potential regional source of these UV-photoprotective compounds for cosmeceutical or biotechnological applications (Vega et al. 2021). Our measurements establish, for the first time in this region, the specific irradiance conditions under which these MAA profiles currently exist and thereby provide a reference

point against which the consequences of ongoing canopy loss can be evaluated. Our findings suggest that MAA-based photoprotection, while present in algae currently living under shaded conditions, cannot be assumed to scale up to compensate for the loss of canopy shade itself. Understanding this limit is essential for anticipating the trajectory of mangrove algal communities under continued canopy loss, and for prioritizing conservation and restoration efforts toward maintaining the shaded microhabitats these chemically distinctive, biodiversity-supporting turf assemblages depend on.

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Declarations

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501 **Competing Interests**

502 The authors declare that they have no known competing financial interests or personal
503 relationships that could have appeared to influence the work reported in this paper.

504 **Availability of data and material**

505 Additional information about study sites and the mean total MAA concentrations are
506 available in table S1 and S2 respectively.

507 **Code availability**

508 The R scripts used for statistical analysis (paired comparisons of irradiance data; Kruskal-
509 Wallis and Dunn's post-hoc tests of MAA content among species) are available from the
510 corresponding author upon reasonable request.

511 **Authors' contributions**

512 **Rossella Nicolai:** Conceptualization, Data curation, Formal analysis, Investigation,
513 Methodology, Supervision, Validation, Visualization, Writing – original draft, Writing –
514 review & editing. **Ulf Karsten:** Conceptualization, Investigation, Supervision, Writing –
515 original draft, Writing – review & editing. **Giuseppe C. Zuccarello:** Investigation,
516 Methodology, Resources, Supervision, Validation, Writing – review & editing. **Shazla**
517 **Mohamed:** Resources, Investigation, Writing – review & editing. **Paolo Galli:**

518 Conceptualization, Funding acquisition, Project administration, Resources, Supervision,
519 Validation, Writing – review & editing.

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Figure captions

Fig. 1. (a) Location of the Maldives in the Indian Ocean. (b) sampling locations in the Maldives. The Maldivian atolls have been divided into northern, central and southern. Latitudes and longitudes shown on axes. Map generated using QGIS 3.36.3 (QGIS Development Team, 2026).

Fig. 2. Habitat overview: a) sandy embayment and b) muddy, damp substrate with *Rhizophora mucronata* and *B. cylindrica* mangrove trees in Funadhoo, Shaviyani. c) muddy, connected to the port (Huraa, Kaafu) d) embayment with sandy substrate and seagrass meadows; e) coastal, completely exposed mangrove, algae were found on mangrove roots and on surrounding rocky substrate (Goidhoo, Baa).

Fig. 3. Irradiance (PAR: $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$; UVA and UVB: both $\mu\text{W cm}^{-2}$) in shaded (green) versus sun-exposed (orange) microhabitats at the eight islands where MAA-containing algae were sampled. Boxes show the median and interquartile range, whiskers extend to $1.5 \times \text{IQR}$, and points denote values beyond that range. Beneath each island name, H gives the local time of the first reading shown as the range from the earliest to the latest; * indicates that these sets were distributed over more than one day (all within the same sampling period). Because measurements were not all taken at solar noon, absolute values partly reflect time of day; shaded and sun-exposed positions at a given island were nevertheless measured within minutes of each other, so the within-island contrast is unaffected. Islands are shown separately and are not pooled; the two Goidhoo sites (Baa and Shaviyani atolls) are distinct islands.

Fig. 4. Morphology and growth habits of *Bostrychia tenella* and *B. binderi*. a, b) corticated main axis. c) long monosiphonous laterals with multiple discoid plastids and (d) abundant, feathery laterals typical of *B. tenella* in contrast to e, f) short and sparse spine-like

laterals of *B. binderi* (f). g, h) photos of *B. tenella* and i) *B. binderi* growing on mangrove roots.

Fig. 5. Morphology and growth habit of *Wilsonosiphonia fujiae*. a) Transverse section with 14 pericentral cells around the axial cell. b) branched multicellular rhizoid. c) Numerous branched trichoblasts at the apex of some axes. d) growth habit of *W. fujiae*. e, f) *W. fujiae* growing in rock crevices (e) and *Bruguiera cylindrica* knee roots (f). Scale bars = 0.1 mm.

Fig. 6. Additional algal taxa collected as incidental specimens. a, b) *Pterocladia caerulea* (Gelidiaceae): (a) percurrent, terete axis apex; (b) pinnately to distichously branched thallus habit. (c) *Gelidiella fanii* (Gelidiellaceae): stolon-like, creeping axis, with a cylindrical to compressed main axis bearing slender branchlets. (d, e) *Laurencia* sp. (Rhodomelaceae): (d) compressed, corticated axis of polysiphonous construction, with a refractile 'corps en cerise' visible within cortical cells; (e) overall thallus habit. (f, g) *Champia* sp. (Champiaceae): (f) hollow, constricted terete axis, with internal transverse diaphragms dividing the thallus into chambers; (g) hemispherical tetrasporangial conceptacles (200–450 μ m diameter) scattered over the segment surface. h, i) *Jania* sp. (Corallinaceae): (h) densely, mostly dichotomously branched tufted habit; (i) articulated construction, showing alternating calcified intergenicula and flexible, uncalcified genicula. Scale bars = 0.1 μ m (a, d, f, g, i).

Fig. 7. MAA composition (concentration, mg g⁻¹ DW) per sample, grouped by species. Error bars show individual samples ordered by total MAA concentration within each species group; stacked segments indicate the mean concentration of each MAA (Porphyra-334, Palythine, Asterina-330, Shinorine); error bars represent $\pm$ 1 SD across replicate injections of the same sample. Site (island, atoll) is indicated below each bar.

Fig. 8. Representative HPLC-DAD chromatograms (DAD1 A, Sig=330 nm) of mycosporine-like amino acids (MAAs) in mangrove-associated red algae across sites and species: *Bostrychia tenella* (HA5TB1, Haa Alifu/Thakandhoo; SH9FB1.3,

Shaviyani/Funadhoo), *Bostrychia binderi* (HA3BB1.3, Haa Alifu/Baarah), *Pterocladiaella*
caerulescens (SH14FPTERO, Shaviyani/Funadhoo), and *Wilsonosiphonia fujiiae* (SH14FW,
Shaviyani/Funadhoo). All panels share the same retention-time axis (0–10 min) to allow
direct comparison of peak position across samples and species; the mAU (y-axis) scale is
independent per panel. Peak identities follow the abbreviation key below; unlabeled peaks (?)
could not be assigned to a compound identity. This panel is included only to illustrate
representative peak morphology.

Table captions

Table 1. Distinct unidentified ("unknown") mycosporine-like amino acid peaks, ordered by
lambda-max, with the species and samples in which each was detected

Supplementary Tables

Table S1. Islands and atolls sampled for this mycosporine-like amino acid (MAA) survey,
with the number of samples analysed from each island.

Table S2. Lambda-max, retention time, and mean concentration of all quantified
mycosporine-like amino acids (MAAs), by sample, alongside the retention time of the
matching standard run in the same batch

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- [TableS1.docx](#)
- [TableS2.docx](#)