The benthic marine algae of the Maldives: historical insights into their diversity and distribution

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Abstract

In tropical ecosystems worldwide, benthic marine algae are important primary producers and habitat providers for many juvenile fish and invertebrate species. Calcified species are known to provide structural support to their respective communities, thus enhancing the overall system's productivity. In the Republic of the Maldives, algae are an important yet currently poorly studied biological resource. We reviewed the literature around algal diversity and distribution across Maldivian atolls and compiled an extensive and updated taxonomic list. The list contains 353 species, of which 31 are Cyanobacteria, 26 Phaeophyceae, 109 Chlorophyta, and 187 Rhodophyta. Algal collections have been reported from only 11 out of 26 atolls, and these mostly occurred during 20th century expeditions. The taxonomic status of 110 species has changed since first reported. While several species have been documented from the country, identifications have thus far almost solely relied on morphological assessments. Many of the reported algal groups require molecular confirmation. This suggests that benthic algal diversity from the Maldives is likely an underestimate. Since anthropogenic activities can significantly altern algal community dynamics, a baseline understanding of algal diversity is necessary to determine how such shifts affect the ecosystem as a whole, thus underpinning future management and conservation efforts.

Keywords

Benthic marine algae; Tropical algae; Algal Diversity and Distribution; Maldives; Maldives Biodiversity;

1. Introduction

The Republic of the Maldives (Maldives) is a small island developing state located in the Indian Ocean (di Biase and Maniku 2021). The country is an archipelago formed by more than 1192 islands that are geographically distributed into 26 natural atolls, spread over 820 km from the northernmost point of Ihavandippolhu (7.006” N) to the southernmost point of Addu atoll (0.042” S), and 80 to 120 km East to West (Dryden et al. 2020). The total land area of 227 km^2 covers less than 1% of the entire area of the country (Dhunya et al. 2017). Therefore, with limited agricultural land and freshwater, the country heavily relies on marine and coastal areas for food, resources and livelihoods. Indeed, marine biological diversity in the Maldives contributes to 71% employment, 89% of Gross Domestic Product and 98% of exports, with many industries that directly benefit from biological resources, including fisheries, tourism and handicrafts (Duvat et al. 2020). However, many important biological resources from Maldives are currently still poorly studied. Among these are the algae, photosynthesizing organisms known to provide essential services to ecosystems worldwide (Stevenson, 2014). Being primary producers, algae play an important role in nutrient cycling and habitat provision for invertebrates within the reef and lagoon systems from tropical regions (Omer et al. 2021). For example, algal species with complex three-dimensional structures, such as those in the genus *Halimeda* J. V. Lamouroux, exert a great influence on other components of community assemblages primarily through non-trophic interactions, i.e. by modification of the physical environments via their own complex structure (McNeil et al. 2021). Benthic primary producers are also known to alter the concentration of minerals and nitrogen in the water column through mineralization and nitrification-denitrification processes

(McGlathery et al. 2007). Some groups of algae can deposit calcium carbonate in their cell walls (Schubert et al. 2020). This them a hard and rigid structure that plays a key role in cementing the reef structures and filling cracks (Lin et al. 2023). There is also evidence that coralline species, such as *Hydrolithon onkodes* (Heydrich) Penrose *et* Woelkerling, promote larval settlement of key benthic invertebrates, including corals (Perrine et al. 2023), thus playing an important role in coral population recovery and reef resilience (Jeong et al. 2023).

The Maldives is currently facing several environmental threats, including the destruction of habitats such as reefs, lagoons, beaches, and mangroves due to land reclamation, harbor building, and many related infrastructure development activities (MEE, 2015). These activities can substantially impact the environment, potentially altering ecosystem dynamics and leading to local extinctions. As a result of human impacts and climate change, algae are known to be declining from coastal regions world-wide (Smale et al. 2019). Moreover, changes in the distribution and composition of algal species, resulting primarily from higher sea surface temperatures, are globally expected to compromise the biodiversity and functioning of ecosystems, because species that provide shelter and food, and reduce environmental stress for other species, thus contributing to the cycling of energy and matter (Martínez et al. 2018), are being replaced by species with different ecological roles. For example, the effects of global warming on seaweed communities are commonly observed to induce a shift toward "turf-forming" algae (Straub et al. 2019). The term "algal turf", is typically used to describe multispecies assemblages of benthic filamentous algae between 1-10 cm in height (Connell et al. 2014). In healthy tropical coral reef assemblages, turf algae form an important component of the epilithic algal community or epilithic algal matrix and

contribute considerably to the total primary productivity and trophic transfer, especially in lagoon, reef flat, and back-reef habitats (O'Brien and Scheibling, 2018). However, under climate change conditions and anthropogenic pressures, such as increased temperatures, sedimentation and nutrient levels, these algae can overgrow neighboring corals, and are therefore associated with a degraded reef state (Straub et al. 2019; Sura et al. 2019).

Data on the diversity and distribution of species spatially and temporally, particularly from poorly studied regions, becomes therefore important to understand the consequences of such future changes on the overall ecosystem function, and therefore to effectively guide environmental management practices. Records of algal diversity from the Maldives are highly sporadic, and currently no comprehensive and up-to-date list of algal diversity from the country is available. The number of algal species present in the Maldives is also inconsistently reported. For example, Dhunya et al. (2017) report 321 species, in 2015 the Maldivian Ministry of Environment and Energy reported 285 algae (21 species of Cyanophyta, 163 Rhodophyta, 83 Chlorophyta, and 18 Phaeophyceae), and more recently Dryden et al. (2020) report the presence of 280 species. These counts primarily refer to a list provided by the major algal survey conducted by Hackett (1977), which resulted from the Cruise B R/V *Te Vega* expedition to nine atolls conducted in 1964. However, many government reports do not account for the more recent study by Payri et al. (2012), and they do not include additional data from other important historical references, such as those resulting from the Percy Sladen Trust Expedition (1899-1900) to Seenu and Gaafu atolls, and the D.R. Stoddart expedition (1964) to Seenu. Moreover, since these observations were made before molecular data of the species was available, and given the high cryptic diversity that is increasingly being

recognized among algal taxa (Miranda Coutinho et al. 2022; Zuccarello et al. 2018), it is plausible that many of these early identifications are inaccurate or have now changed taxonomic status.

The aim of this review is therefore to provide a comprehensive and up-to-date list of macroalgal species that have been described from the Maldives, in order to aid future molecular work, and to gather information about the species distribution across different atolls, based on information provided from historical records. Understanding the changes in algal community composition that may have occurred in space and time can provide important information to elucidate the effects of anthropogenic activities on the marine biodiversity of the country. Ultimately, this information can contribute to more effective conservation and management practices.

2. Methods

2.1. Taxonomic data.

The dataset for the species of benthic algae in the Maldives was downloaded from Algaebase (https://www.algaebase.org/), a global database of taxonomic and distributional information on algae (Guiry and Guiry, 2014). Several key papers (Table 1) and the book "Benthic algae of the Indian Ocean" by Silva et al. (1996) were consulted to obtain the names for all species currently reported from the country. The current nomenclatural status of all species in the list was checked on AlgaeBase and updated as needed.

The list provided by Algaebase included several microalgal species identified by Stanca et al. (2013), the majority of which are phytoplankton. Since the present list only includes benthic algae, these species were removed from the final list, except for the genus *Spirulina* Turpin ex Gomont (cyanobacteria), which contains several mat-forming, benthic species.

Many entries in previous lists were only identified to genus. These genus-level identifications were not considered in the final list and counts, because they were considered not to be sufficiently identified (e.g., "*Halimeda* sp.", "*Amphiroa* sp". in Payri et al. 2012). However, some of these unresolved identifications were maintained in the present list in order to include genera that would otherwise not be represented (i.e., lack of species-level identifications for the genus *Acetabularia* J.V. Lamouroux). When multiple identifications at the genus level were listed as multiple species (e.g., *Rhodymenia* sp. 1, sp. 2, sp. 3, sp. 5 in Payri et al. 2012), only one entry representative of the genus was included in the list.

2.2. Distribution data

The literature was consulted to obtain insights into which atolls were visited during the different expeditions and where the algal specimens were collected. Information about the historical expeditions and in which atolls algal collections were made is reported in Table 1. Herbarium specimens were also consulted to obtain further insights into the species diversity and distribution. The data from these was retrieved from the Macroalgal Herbarium Portal (www.macroalgae.org), a public digital repository of

scanned herbarium collections from the last 150 years (Macroalgal Herbarium Portal 2020).

Table 1. Previous expeditions conducted in the Maldives that resulted in the collection and reporting of benthic marine algae. The references indicate the articles published following each expedition, used to compile the present list.

Expedition Name	Year	Atolls	Collected By	Reference
Percy Sladen Trust Expedition	1899-1900	Seenu, Suvadiva	Gardiner, J.S.	Barton (1903); Foslie (1903); Foslie (1907); Gardiner (1903); Weber van Bosse and Foslie (1904); Weber van Bosse (1914)
John Murray Expedition	1933-1934	Kardiva Channel	Newton, L.M.	Newton (1953)
D.R. Stoddart	1964	Addu (Seenu)	Sigee, D.	Sigee (1966); Tsuda and Newhouse (1966); Hollenberg (1968a); Hollenberg (1968b)
Cruise B R/V Te Vega	1964	Dhaalu, Kaafu, Laamu, Northern Ari, Haa Alifu, Lhaviyani, Noonu, Raa, Seenu	Hackett, H.E. and Rhyne, C.	Hackett (1977); Wynne (1993)
U.S. Navy Biological Expedition	1967	Addu (Seenu)	Rhyne, C.	Hackett (1977)
NA	1976	Dhaalu, Noonu	Titlyanova and Butorin	Titlyanova and Butorin (1978)
NA	2012	Baa	Payri et al.	Payri et al. (2012)
NA	2013	Faafu	Stanca et al.	Stanca et al. (2013)

3. Results

3.1. Algal diversity in the Maldives

The AlgaeBase search yielded 326 names of species reported from the Maldives. These database entries reference the "Catalogue of the Benthic Marine Algae from the Indian Ocean" (Silva et al. 1996) and the phytoplankton species identified by Stanca et al. (2013). The names reported in the comprehensive 'Catalogue' provided in turn reference articles resulted from collections made during the 20th century expeditions to the country. After cross-checking these references, 117 species that have been reported by Hackett (1977), Tsuda and Newhouse (1966), and Payri et al. (2012) were missing from the list provided by Algaebase when searching for algae from the Maldives.

The current updated list contains 353 species, of which 31 are Cyanobacteria, 26 Phaeophyceae, 109 Chlorophyta, and 187 Rhodophyta (Appendix 1). Of these, 110 taxonomic names have changed since they were first reported. The updated taxonomy reveals a higher diversity of genera than previously reported, mostly due to genera being split since their original cataloguing. For example, following the older taxonomy of the family Peyssonneliaceae reported from the Maldives, two genera (*Peyssonnelia* Decaisne and *Cruoriella* P.L. Crouan *et* H. M. Crouan) from this family were reported. Within these genera however, the currently accepted taxonomic classification of what were historically reported as *Peyssonnelia rubra* f. *orientalis* Weber Bosse, *P. Calcea* Heydrich, and *P. capensis* Montagne reveals that they belong to three different genera in this family (*Agissea orientalis* (Weber Bosse) Pestana, Lyra, Cassano J.M.C,

Ramicrusta Calcea (Heydrich) K.R. Dixon *et* G.W. Saunders, and *Sonderophycus capensis* (Montagne) M.J. Wynne, respectively; Pestana et al. 2021). Similarly, in the Rhodomelaceae, the species currently accepted as *Vertebrata foetidissima* (Cocks ex Bornet) Díaz-Tapia *et* Maggs and *Wilsonosiphonia howei* (Hollenberg) D. Bustamante, Won et T.O. Cho, *Melanothamnus upolensis* (Grunow) Díaz-Tapia *et* Maggs, *M. sphaerocarpus* (Børgesen) Díaz-Tapia *et* Maggs, *M. savatieri* (Hariot) Díaz-Tapia *et* Maggs and *Kapraunia pentamera* (Hollenberg) Savoie *et* G.W. Saunders were all previously placed in the genus *Polysiphonia* Greville, although the achievement of monophyletic groups among Rhodomelaceaean tribes remains difficult (Díaz-Tapia et al. 2017; Savoie and Saunders 2019). A recent study by Boo et al. (2020) also revealed the occurrence of *Wilsonosiphonia fujiae* D. Bustamante, Won et T.O. Cho in the atolls in the islands of Fulhadoo (Baa atoll) and Dhidhdhoo (Alifu Dhaalu). In some cases, the updated taxonomy for particular groups results in less species compared to the historical reports being included in the present list. For example, for the species currently accepted as *Neogoniolithon brassica-florida* (Harvey) Setchell et L.R. Mason, which was previously regarded as five separate species and variants in two different genera (i.e., *Goniolithon frutescents* Foslie, *Goniolithon frutescens f. congestum* Foslie, and *Goniolithon laccadivum* Foslie*,* Hackett, 1977; *Neogoniolithon brassica-florida* (Harvey) Setchell et L.R. Mason, and *Neogoniolithon laccadivum* (Foslie) Setchell et L.R. Mason, Payri et al. 2012) that are now all regarded as one species (Kato et al. 2013; Villas-Bôas et al. 2015).

The search on the “Macroalgal Herbarium Collection" website yielded 819 results of herbarium vouchers of specimens from the Maldives. The vast majority of these vouchers was collected during the 1964 Cruise B R/V *Te Vega* expedition and deposited

in different herbaria by H.E. Hackett. Often, multiple vouchers of the same species were deposited from the same location. Some of the vouchers available on the website were deposited by Gardiner (1903; Kaafu atoll), Sigee (1966; Seenu atoll), and Wynne (1964; Kaafu atoll). The Macroalgae Herbarium Portal data also included notes that were used to obtain information about the diversity of species that form “turfs" and those associated with mangroves. In the list published by Hackett (1977), the author reports the presence of the genera *Gelidium* J.V. Lamouroux. and *Jania* J.V. Lamouroux (Rhodophyta), and the species *Caulerpa racemosa* var. *macrophysa* (Sonder ex Kützing) W. R. Taylor (Chlorophyta) in association with the prop roots of the mangrove *Rhizophora mucronata* Poir. However, in the notes written by the author on the herbarium specimens available on the Macroalgae Herbarium Portal website, the genus *Herposiphonia* Nägeli (Rhodophyta), and the cyanobacteria species *Anabaena oscillarioides* Bory ex Bornet *et* Flahault, and *Hydrocoryne soluta* (Bornet *et* Grunow) were also reported to be found in association with mangroves.

3.2. Distribution Data

Benthic algal species have been reported from 11 out of the 26 atolls in the country. These algae have been collected in four northern (Baa, Payri et al. 2012; Haa Alifu, Lhaviyani, Noonu, Raa, Hackett, 1977) and four central (Dhaalu, Kaafu, Laamu, and Northern Ari, Hackett 1977) atolls (Fig. 1). Out of the three atolls in the southern region, algae species have only been collected in Seenu (Hackett, 1977, Sigee 1966). The atolls of Kaafu, Baa, and Seenu show the highest number of algal species reported, with 131, 148, and 144 species, respectively (Fig. 1).

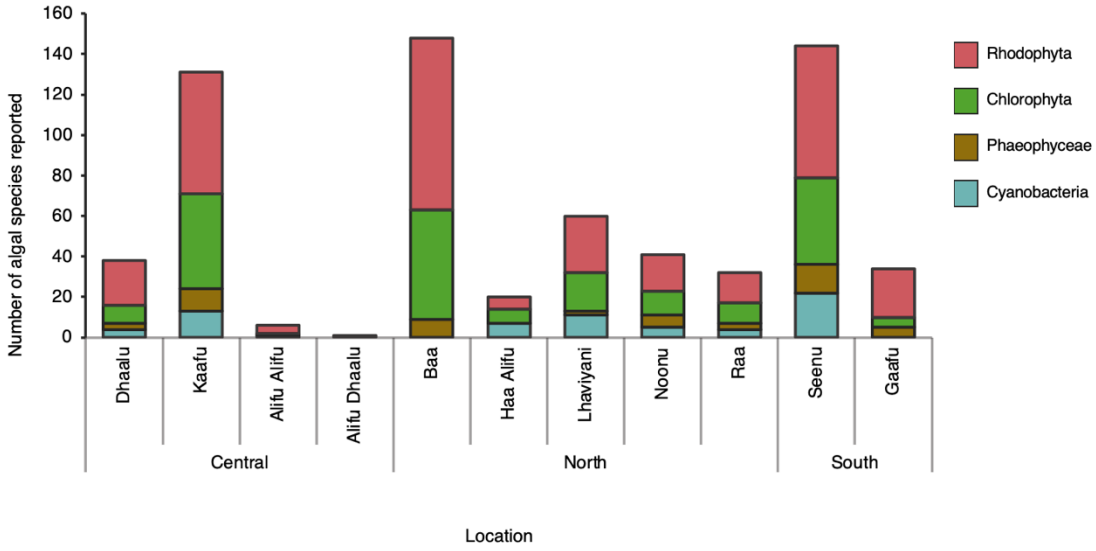

Figure 1. Number of benthic algal species, divided by major groups (Cyanobacteria, Phaeophyceae, Chlorophyta, Rhodophyta), reported from Central, Northern, and Southern locations.

The earliest collections of algae in the Maldives were made during the Percy Sladen Trust expedition of 1899-1900, under the leadership of John Stanley Gardiner, which resulted in the record of nine species in the Corallinaceae (Rhodophyta) and six species of green and brown algae in the atolls of Seenu (Addu) and Huvadhoo (Suvadiva) (Foslie, 1903; Barton, 1903). From this expedition, other species of Chlorophyta and Rhodophyta were reported by Weber van Bosse (1914) and six more articles were published (Table 1). After the last article from this expedition was published by Weber van Bosse, no studies reported on the diversity of algae in the Maldives until Newton (1953), which provided identifications of species collected during the 1933-1934 crossing of the Kardiva Channel, a channel between the Northern and Central Maldivian atolls, during the J. Murray Expedition. This resulted in ten more species collections

(one Cyanobacteria, two Phaeophyceae, four Chlorophyta, three Rhodophyta). The D.R. Stoddart Cambridge expedition (1964) to Addu atoll resulted in two new lists (Sigee 1966; Tsuda and Newhouse 1966), which added seven Cyanobacteria, 20 Rhodophyta, 25 Chlorophyta, and seven Phaeophyceae species to the list of known algae. Two more studies were published after the D.R. Stoddart expedition of 1964, although these only reported single accounts of the red algal genera *Herposiphonia* Nägeli and *Polysiphonia* Greville (Hollenberg 1968a, b). In 1964, Hackett extensively studied the benthic algal diversity of nine Maldivian atolls (Table 1), which he visited during the International Indian Ocean Expedition, Cruise B of the R/V *Te Vega.* In his 1977 article, he listed all the species collected and identified and also reported the species collected during the U.S. Navy Biological Expedition to the Chagos in 1967, collected by C. Rhyne at Addu atoll. In the last 20 years, only the article published by Payri et al. (2012) studied the diversity of benthic algae in the Maldives, while the article published by Stanca et al. (2012) focused on the diversity of phytoplankton species.

4. Discussion

The present review is the first report compiling the benthic algal diversity of the Maldives as presently known. Our extensive checklist also updates the taxonomic classification for these species and gathers information about their distribution across atolls. Our results show that 111 species names of benthic marine algae in the Maldives reported in the literature are outdated and that their taxonomic status changed since they were first reported. The collections of benthic algae are also very uneven and occurred from only 11 out of the 26 atolls in the country. The bulk of publications regarding the

diversity of benthic algae from the country dates back to the first half of the 20th century, while only one study on algal diversity was conducted in the last twenty years. Since most collections were made before molecular data was available, almost all specimens were identified based on morphological traits without any molecular validation.

4.1. Historical algal explorations in the Maldives

In the 20th century, a series of oceanographic studies were conducted to explore different aspects of the biodiversity of the Maldives. During these expeditions, benthic algal samples were collected primarily by snorkeling or by SCUBA to depths of 10 m. The samples were typically processed into dried herbarium specimens, or preserved in formalin, for further identification.

While the Percy Sladen Trust Expedition conducted in 1899-1900 in the atolls of Seenu (Addu) and Huvadhoo (Suvadiva) resulted in the highest number of publications that report the presence of algae in the Maldives, the collections made during this expedition were sporadic and the published articles only described a few algal specimens. The most extensive sampling, in terms of distribution range and quantity of specimens collected, was carried out by Hackett in 1964. He collected algae from nine different atolls across the country (Dhaalu, Kaafu, Laamu, Northern Ari, Haa Alifu, Lhaviyani, Noonu, Raa, Seenu) as part of a PhD project. In an article published in 1977, the author reported the presence and distribution of 205 species. A more recent major survey of benthic algae in the Baa Atoll by Payri et al. (2012), but molecular analysis of the algal tissue collected

was only carried out for samples of Dictyotales (*Dictyota* J.V. Lamouroux, *Padina* Adanson) and *Halimeda*.

While several collections of algae were made during these expeditions to the Maldives, information about the algal diversity of the country remains sporadic and incomplete. Moreover, with the exception of the 1964 Cruise B R/V *Te Vega* Expedition, algal collections were only made from a few sites within single atolls.

Not all algal groups were always considered in previous surveys. For example, while Payri et al. (2012) brought the total number of species to 321 (200 Rhodophyta, 97 Chlorophyta, and 24 Phaeophyceae), the authors did not include Cyanobacteria. This group of algae, however, was included in previous counts of algae from the Maldives (Hackett 1977, Sigee 1966, Tsuda and Newhouse 1966). Cyanobacteria were maintained in the present list, on the basis that these microscopic organisms are able to form mats that are visible to the naked eye and can be collected in a similar way as macroalgal species. For example, herbarium specimens of cyanobacteria samples collected by Hackett in the 1964 expedition were available on the "Macroalgae Herbarium Portal".

4.2. Lack of molecular evidence

Correctly identifying algal specimens based on morphological traits requires a significantly high degree of training. As historical observations were based on the

morphological identification only, it must be assumed that previous collectors were sufficiently competent to judge critical differences between the specific entities represented. But still many identifications were in fact not resolved below the genus level, possibly because of a lack of identifying structures (e.g., reproductive parts) or lack of expertise in the investigators. Moreover, molecular techniques have only started revealing the cryptic diversity amongst algae (e.g., Payo et al. 2013) and also revealed incorrect taxonomy in many similar taxa (D'Archino et al. 2015, 2017). Based on the lack of systematic sampling and molecular evidence, it is plausible that the diversity of species in the Maldives is seriously underestimated, and that at least some of the previous identifications are incorrect. For example, while the occurrence of *Wilsonosiphonia howei* in the Maldives was reported in 1977 by Hackett, this species is morphologically very similar to *W. fujiae*, a species recently described by Bustamante et al. (2017) and whose occurrence in the Maldives was molecularly confirmed by Boo et al. (2020) using rbcL and COI-5p primers. This raises questions about the true identity of the 1977 specimen, and highlights the need for molecular work to confirm algal identifications.

4.3. Ecological Importance

4.3.1. Calcified algae

Species commonly reported in the Maldives, such as those in the genus *Halimeda*, are known to contribute to structural complexity in coral reefs worldwide, and their structures have been compared to rainforests, with a thick surface undergrowth, mid-layer subcanopy and shrubby canopy up to 30 cm above the seafloor (McNeil et al. 2021). According to the present list, there are 14 species of *Halimeda* reported from the

Maldives. Payri et al. (2012) indicated that the lagoon reef flats and slopes account for many encrusting coralline algae, mostly represented by the genera *Hydrolithon* (Foslie) Foslie and *Lithophyllum* Philippi. These ecologically important calcareous groups are almost certainly underrepresented by historical studies. Molecular tools are in fact essential to the correct taxonomical classification of these entities, particularly the encrusting forms, as DNA sequence data and phylogenetic analyses have led to major insights in the diversity and evolutionary history of the group (Jeong et al. 2021). These families are increasingly found to have a high degree of cryptic diversity, with studies actively revisioning their classification at species level and above (e.g., Nelson et al. 2015; Cremen et al. 2016; Pestana et al. 2021; Coutinho et al. 2022).

4.3.2. Turf algae

In the Maldives, turf algae are typically mentioned in government reports in the context of a system change toward algal-turf-dominated systems taking over the reef in response to cyclones and bleaching events, such as the one that notably impacted the Maldives in 1998 (MEE, 2015; Dhunya et al. 2017). However, the term is often used in a broader context, as many different species are capable of forming “turfs”. In Hackett’s herbarium notes, for example, there are 34 different genera reported as “turf”, including species in the Rhodophyta, Chlorophyta, Phaeophyceae, and cyanobacteria. Under healthy environmental conditions, these algae are essential components of reef systems. For example, they contribute significantly to the gross primary productivity, and the cyanobacteria species provide nitrogen to the systems through the fixation of atmospheric nitrogen (Bender et al. 2014). However, when compared to coralline algae and calcified macroalgae, turf algae can grow faster and can weaken and eventually overgrow neighboring corals, and hence they are increasingly seen to take over degraded coral reefs globally (O’Brien and Scheibling, 2018). Understanding the

species composition of these algal communities could therefore provide important information about the health status of the reefs in the Maldives.

4.3.3. Mangrove-associated algae

There are almost no reports of algae associated with mangroves in the Maldives (Cerri et al. 2023). However, mangrove-associated algae are globally known to enhance the productivity of these important ecosystems, contributing to nutrient cycling and providing an additional source of food to many species (Gao and Lin 2018; Omer et al. 2021). Mangroves around the world are known to host a macroalgal species complex named the "Bostrychietum" after the genus *Bostrychia* Montagne, which is commonly observed in these habitats (Post et al. 1936), but the term also includes the red algal genera *Catenella* Greville and *Caloglossa* (Harvey) G. Martens. While these genera have not yet been reported from the Maldives, they have been observed in mangroves from other locations in the Indian Ocean (Lambert et al. 1987; Steinke and Naidoo 1990; Phillips et al. 1996; Kandaswamy et al. 2018). Members of the "Bostrychietum" are often exposed in the mangroves to strong environmental stressors as they experience diurnal tidal immersion-emersion cycles (e.g. West et al. 1992). *Bostrychia* and *Caloglossa* species synthesize and accumulate rather unusual polyols as organic osmolytes and these compatible solutes compensate salinity changes, as well as containing a widely variety of UV-sunscreen compounds (Karsten et al. 1996, 2000). These biochemical capabilities contribute to the pronounced stress tolerance of these red algae, and are increasingly gaining attention for potential commercial applications (Messina et al. 2019, Sun et al. 2020).

4.1. Lack of data

While at least some information on benthic macroalgae and cyanobacteria in the Maldives exist, other benthic algal groups such as microphytobenthic communities which are often dominated by pennate diatoms are completely unstudied. From an ecological standpoint microphytobenthic assemblages exert an important function in coastal waters, as they strongly contribute to the marine primary production and biogeochemical cycling of nutrients (Cahoon, 1999), to sediment stabilization by excreting sticky extracellular polymeric substances (EPS) (De Brouwer et al. 2005) and as a food resource for benthic suspension- or deposit-feeders (Cahoon, 1999). Therefore, knowledge on the occurrence and diversity of benthic diatoms in the Maldives is needed.

Conclusions

The present review provides an extensive and updated taxonomic list of algal species diversity and distribution across Maldivian atolls. Our findings highlight the lack of molecular studies confirming the identity of algal species historically reported from the country. Accurate information about the community composition of algae from the reef and mangrove habitats of the country would provide important insights into the primary productivity of these habitats, thus significantly contributing to our understanding of the overall system functioning. Moreover, understanding how species communities may have changed over time would elucidate the effects of anthropogenic pressures on the biodiversity of these systems. Finally, algae are increasingly recognized as an untapped marine source of bioactive molecules with diverse applications. However, the chemical

profile of algae, and methods of analysis, can be highly variable across species. The present review provides important information to guide future studies exploring the commercial potential of algae from the Maldives.

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Author Contributions

Prof. Galli secured funding and resources necessary for conducting the review. Rossella Nicolai conceived the idea of the article, conceptualized the manuscript, performed the literature search, data analysis and wrote the first draft. Prof. Joe Zuccarello and Prof. Ulf Karsten contributed their expertise and critically revised the manuscript, ensuring the accuracy and depth of the review. All authors contributed to writing different sections and participated in the review and editing of the manuscript, ensuring adherence to journal guidelines.

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Conflict of interest statement

The authors have no relevant financial or non-financial interests to disclose.

Compliance with ethical standards

No samples were collected for the present review. All species names presented in the final list, and the databases they were obtained from, are referenced.

Reference list

Barton, E.S. (1903). List of marine algae collected at the Maldive and Laccadive Islands by JS Gardiner Esq., MA. *Bot. J. Linn*. *35*: 475–482.

Bender, D., Diaz-Pulido, G., Dove, S. (2014). Warming and acidification promote cyanobacterial dominance in turf algal assemblages. *Mar. Ecol. Prog. Ser*. *517*: 271–284.

Boo, G.H., Cho, T.O., Sherwood, A.R., Boo, S.M., Fujii, M.T. (2020). Discovery of *Wilsonosiphonia fujiae* (Rhodomelaceae, Rhodophyta) from the Maldives Islands and transfer of *Polysiphonia rhizoidea* from Hawai'i to *Wilsonosiphonia*. *Phytotaxa 451*: 63–72.

Bustamante, D.E., Won, B.Y., Miller, K.A., Cho, T.O. (2017). *Wilsonosiphonia* gen. nov. (Rhodomelaceae, Rhodophyta) based on molecular and morpho-anatomical characters. *J. Phycol*. *53*: 368–380.

Cahoon, L., 1999. The role of benthic microalgae in neritic ecosystems. *Oceanog. Mar. Biol. 37*: 47–86.

Cerri, F., Louis, Y.D., Fallati, L., Siena, F., Mazumdar, A., Nicolai, R., Zitouni, M.S., Adam, A.S., Mohamed, S., Lavorano, S., Galli, P., 2024. Mangroves of the Maldives: a review of their distribution, diversity, ecological importance and biodiversity of associated flora and fauna. *Aquat. Sci. 86*: 44.

Connell, S.D., Foster, M.S., Airoldi, L. (2014). What are algal turfs? Towards a better description of turfs. *Mar. Ecol. Prog. Ser*. *495*: 299–307.

Coutinho, L.M., Nasri Sissini, M., Vieira-Pinto, T., Muller De Oliveira Henriques, M.C., Oliveira, M.C., Antunes Horta, P., Barbosa De Barros Barreto, M.B. (2022). Cryptic diversity in non-geniculate coralline algae: a new genus *Roseolithon* (Hapalidiales, Rhodophyta) and seven new species from the Western Atlantic. *Eur. J. Phycol*. *57*: 227–250.

Cremen, M.C.M., Huisman, J.M., Marcelino, V.R., Verbruggen, H. (2016). Taxonomic revision of *Halimeda* (Bryopsidales, Chlorophyta) in south-western Australia. *Aust. Syst. Bot*. *29*: 41–54.

De Brouwer, J.F.C., Wolfstein, K., Ruddy, G.K., Jones, T.E.R., Stal, L.J. (2005). Biogenic Stabilization of Intertidal Sediments: The Importance of Extracellular Polymeric Substances Produced by Benthic Diatoms. *Microb. Ecol. 49*: 501–512.

Dhunya, A., Huang, Q., Aslam, A. (2017). Coastal habitats of Maldives: status, trends, threats, and potential conservation strategies. *Int. J. Sci. Eng. Res. 8*: 47–62.

Di Biase, R., Maniku, A.A. (2021). Transforming Education in the Maldives: The Challenges of a Small Island Developing State, in: Sarangapani, P.M., Pappu, R. (Eds.). *Handbook of Education Systems in South Asia*, *Global Education Systems*. Springer Singapore, Singapore, pp. 545–573.

Díaz-Tapia, P., Maggs, C.A., West, J.A., Verbruggen, H. (2017). Analysis of chloroplast genomes and a supermatrix inform reclassification of the Rhodomelaceae (Rhodophyta). *J. Phycol. 53*: 920–937.

Dryden, C., Basheer, A., Grimsditch, G., Musthaq, A., Newman, S., Shan, A. (2020). A rapid assessment of natural environments in the Maldives. Gland, Switzerland: IUCN and Government of Maldives.

Duvat, V.K.E., Magnan, A.K., Perry, C.T., Spencer, T., Bell, J.D., Wabnitz, C.C.C., Webb, A.P., White, I., McInnes, K.L., Gattuso, J., Graham, N.A.J., Nunn, P.D., Le Cozannet, G.

(2021). Risks to future atoll habitability from climate-driven environmental changes. *WIRE: Climate Change 12*: e700.

Foslie, M.H. (1907). The Lithothamnia. In Gardiner, J.S. 1907-1936. Percy Sladen Trust Expedition to the Indian Ocean in 1905. *Tran. Linn. Soc. Lond. 2nd Series: Zoology 1*: 177–192.

Foslie, M.H. (1903). The Lithothamnia of the Maldives and Laccadives. In J.S. Gardiner (ed.) *The fauna and geography of the Maldive and Laccadive Archipelagoes. Being the account of the work carried on and of the collections made by an expedition during the years 1899 and 1900*. Vol. I., Cambride University Press, Cambridge, pp. 460–471.

Gao, Y., Lin, G. (2018). Algal diversity and their importance in ecological processes in typical mangrove ecosystems. *Biod. Sci. 26*: 1223–1235.

Gardiner, J.S. (1903). *The fauna and geography of the Maldive and Laccadive archipelagoes : being the account of the work carried on and of the collections made by an expedition during the years 1899 and 1900*. *Vol. I., II*. Cambridge University Press, Cambridge.

Guiry, M.D. and Guiry, G.M. (2014) AlgaeBase. World-wide Electronic Publication, National University of Ireland, Galway. http://www.algaebase.org.

Hackett, H.E. (1977). Marine algae known from the Maldive Islands. *Atoll Res. Bull*.

Hollenberg, G.J. (1968a). An account of the species of *Polysiphonia* of the central and western tropical Pacific Ocean. I. *Oligosiphonia*. *Pac. Sci. 22*: 56–98.

Hollenberg, G.J. (1968b). An account of the species of the red alga *Herposiphonia* occurring in the central and western tropical Pacific Ocean. *Pac. Sci. 22*: 536–559.

Jeong, S.Y., Gabrielson, P.W., Hughey, J.R., Hoey, A.S., Cho, T.O., Abdul Wahab, M.A., Diaz-Pulido, G. (2023). New branched *Porolithon* species (Corallinales, Rhodophyta) from the Great Barrier Reef, Coral Sea, and Lord Howe Island. *J. Phycol. 59*: 1179–1201.

Jeong, S.Y., Nelson, W.A., Sutherland, J.E., Peña, V., Le Gall, L., Diaz-Pulido, G., Won, B.Y., Cho, T.O. (2021). Corallinapetrales and Corallinapetraceae: A new order and family of coralline red algae including *Corallinapetra gabrielii* comb. nov. *J. Phycol. 57*: 849–862.

Kandaswamy, G., West, J., Necchi Jr, O. (2018). A catalogue and bibliography of non-marine (freshwater and estuarine) Rhodophyta (red algae) of India. *Phytotaxa 364*: 1–48.

Karsten, U., Barrow, K.D., Nixdorf, O., King, R.J. (1996). The compability with enzyme activity of unusual organic osmolytes from mangrove red algae. *Funct. Plant Biol. 23*: 577–582.

Karsten, U., Sawall, T., West, J., Wiencke, C. (2000). Ultraviolet sunscreen compounds in epiphytic red algae from mangroves. *Hydrobiologia 432*: 159–171.

Kato, A., Baba, M., Suda, S. (2013). Taxonomic circumscription of heterogeneous species *N eogoniolithon brassica-florida* (Corallinales, Rhodophyta) in Japan. *Phycol. Res. 61*: 15–26.

Lambert, G., Steinke, T.D., Naidoo, Y. (1987). Algae associated with mangroves in southern African estuaries. I. Rhodophyceae. *S. Afr. J. Bot. 53*: 349–361.

Lin, S.-M., Nelson, W., Huisman, J.M. (2023). Species diversity and ecological roles of marine calcified macroalgae, with an emphasis on coralline algae in the western Pacific Ocean. *Phycologia 62*: 533–534.

Macroalgal Herbarium Portal. (2024). https://macroalgae.org/portal/index.php. Accessed on July 10.

Martínez, B., Radford, B., Thomsen, M.S., Connell, S.D., Carreño, F., Bradshaw, C.J.A., Fordham, D.A., Russell, B.D., Gurgel, C.F.D., Wernberg, T. (2018). Distribution models predict large contractions of habitat-forming seaweeds in response to ocean warming. Divers. *Distrib. 24*: 1350–1366.

McGlathery, K., Sundbäck, K., Anderson, I. (2004). The importance of primary producers for benthic nitrogen and phosphorus cycling. in: *Estuarine Nutrient Cycling: The Influence of Primary Producers*: The Fate of Nutrients and Biomass. Dordrecht, Springer, pp. 231–261.

McNeil, M., Firn, J., Nothdurft, L.D., Pearse, A.R., Webster, J.M., Roland Pitcher, C. (2021). Inter-reef *Halimeda* algal habitats within the Great Barrier Reef support a distinct biotic community and high biodiversity. *Nat. Ecol. Evol. 5*: 647–655.

Messina, C.M., Renda, G., Laudicella, V.A., Trepos, R., Fauchon, M., Hellio, C., Santulli, A. (2019). From ecology to biotechnology, study of the defense strategies of algae and

halophytes (from Trapani Saltworks, NW Sicily) with a focus on antioxidants and antimicrobial properties. *Int. J. Mol. Sci*. *20*: 881.

Ministry of Environment and Energy. (2015). Maldives Climate change policy framework, Maldives.

Nelson, W.A., Sutherland, J.E., Farr, T.J., Hart, D.R., Neill, K.F., Kim, H.J., Yoon, H.S. (2015). Multi-gene phylogenetic analyses of New Zealand coralline algae: *Corallinapetra Novaezelandiae* gen. et sp. nov. and recognition of the Hapalidiales ord. nov. *J. Phycol. 51*: 454–468.

Newton, Linda M. (1953). Marine Algae. The John Murray Expedition 1933-1934. *Sci. Rep. 9*: 395–420.

O'Brien, J.M., Scheibling, R.E. (2018). Turf wars: competition between foundation and turf-forming species on temperate and tropical reefs and its role in regime shifts. *Mar. Ecol. Prog. Ser. 590*: 1–17.

Omer, M.Y., Abd El-Wakeil, K.F., Hussein, H.N.M., Rashedy, S.H. (2021). Invertebrate assemblages associated with seaweeds at different locations in the red sea, Egypt. *Egypt. J. Aquatic Biol. Fish. 25*: 407–421.

Payo, D.A., Leliaert, F., Verbruggen, H., D'Hondt, S., Calumpong, H., Clerck, O. (2013). Extensive cryptic species diversity and fine-scale endemism in the marine red alga *Portieria* in the Philippines. *Proc. Biol. Sci 280*: 20122660.

Payri, C., N'Yeurt, A. de R., Mattio, L. (2012). Benthic algal and seagrass communities in Baa Atoll, Maldives. In: Andréfouët (Ed.). *Biodiversity, resources, and conservation of*

Baa Atoll (Republic of Maldives): a UNESCO man and biosphere reserve. *Atoll Res. Bull. 590*: 31-70.

Perrine, M.J.S., Mundil, S., Kaullysing, D., Bhagooli, R. (2023). The red coralline alga *Hydrolithon onkodes*, an attractor of coral larvae, is photosynthetically more susceptible to thermal stress than *Lithophyllum incrustans*. *Indo Pac. J. Ocean Life 7*.

Pestana, E.M. dos S., Nunes, J.M. de C., Cassano, V., Lyra, G. de M. (2021). Taxonomic revision of the Peyssonneliales (Rhodophyta): Circumscribing the authentic *Peyssonnelia* clade and proposing four new genera and seven new species. *J. Phycol. 57*: 1749–1767.

Phillips, A., Lambert, G., Granger, J.E., Steinke, T.D. (1996). Vertical Zonation of Epiphytic Algae Associated with *Avicennia marina* (Forssk.) Vierh. Pneumatophores at Beachwood Mangroves Nature Reserve, Durban, South Africa. *Bot. Mar. 39*: 167-175.

Post, E. (1936). Systematische und pflanzengeographische Notizen zur *Bostrychia-Caloglossa*-Assoziation. *Rev. Algol. 9*: 1–84.

Savoie, A.M., Saunders, G.W. (2019). A molecular assessment of species diversity and generic boundaries in the red algal tribes Polysiphonieae and Streblocladieae (Rhodomelaceae, Rhodophyta) in Canada. *Eur. J. Phycol. 54*: 1–25.

Schubert, N., Schoenrock, K.M., Aguirre, J., Kamenos, N.A., Silva, J., Horta, P.A., Hofmann, L.C. (2020). Coralline algae: Globally distributed ecosystem engineers. *Front. Mar. Sci. 7*:352.

Sigee, D.C. (1966). Preliminary account of the land and marine vegetation of Addu Atoll. *Atoll Res. Bull. 116*: 1–122.

Silva, P.C., Basson, P.W., Moe, R.L. (1996). *Catalogue of the Benthic Marine Algae of the Indian Ocean*. University of California Publications in Botany. *79*: 1-1259.

Smale, D.A., Wernberg, T., Oliver, E.C.J., Thomsen, M., Harvey, B.P., Straub, S.C., Burrows, M.T., Alexander, L.V., Benthuysen, J.A., Donat, M.G., et al. (2019). Marine heatwaves threaten global biodiversity and the provision of ecosystem services. *Nat. Clim. Change. 9*: 306–312.

Stanca, E., Roselli, L., Durante, G., Seveso, D., Galli, P., Basset, A. (2013). A checklist of phytoplankton species in the Faafu atoll (Republic of Maldives). *Trans. Wat. Bull. 7*: 133–144.

Steinke, T.D., Naidoo, Y. (1990). Biomass of algae epiphytic on pneumatophores of the mangrove, *Avicennia marina*, in the St Lucia estuary. *S. Afr. J. Bot. 56*: 226–232.
Stevenson, R. (2014). Ecological assessments with algae: A review and synthesis. *J. Phycol. 50*: 437–461.

Straub, S.C., Wernberg, T., Thomsen, M.S., Moore, P.J., Burrows, M.T., Harvey, B.P., Smale, D.A. (2019). Resistance, Extinction, and Everything in Between – The Diverse Responses of Seaweeds to Marine Heatwaves. *Front. Mar. Sci. 6*: 763.

Sun, Y., Zhang, N., Zhou, J., Dong, S., Zhang, X., Guo, L., Guo, G. (2020). Distribution, Contents, and Types of Mycosporine-Like Amino Acids (MAAs) in Marine Macroalgae and a Database for MAAs Based on These Characteristics. *Mar. Drugs 18*: 43.

Sura, S.A., Delgadillo, A., Franco, N., Gu, K., Turba, R., Fong, P. (2019). Macroalgae and nutrients promote algal turf growth in the absence of herbivores. *Coral Reefs 38*: 425–429.

Titlyanova, T.V., Butorin, P.V. (1978). Algae of the Maldive and Seychelles Islands. In: *Biology of coral reefs: photosynthesis of Zooxanthellae*. Institute of Marine Biology, Far East Science Center, Academy of Sciences of the USSR, Vladivostok. *Transactions 12*: 19–28.

Tsuda, R.T., Newhouse, J. (1966). Marine benthic algae from Addu atoll, Maldive Islands. In D.R. Stoddart (ed.), Reef studies at Addu Atoll, Maldive Islands, Preliminary results of an expedition to Addu Atoll in 1964. *Atoll Res. Bull. 116*: 1–122.

Villas-Boas, A.B., Riosmena-Rodriguez, R., Tamega, F.T., Amado-Filho, G.M., Maneveldt, G.W., Figueiredo, M.A. (2015). Rhodolith-forming species of the subfamilies Neogoniolithoideae and Hydrolithoideae (Rhodophyta, Corallinales) from Espírito Santo State, Brazil. *Phytotaxa 222*: 169–184.

Weber Van Bosse, A., Foslie, M.H. (1904). The Corallinaceae of the Siboga Expedition. Siboga Expeditie. E. J. Brill, Leyden. *61*

Weber Van Bosse, A. (1914). The Percy Sladen Trust Expedition to the Indian Ocean in 1905, under the leadership of Mr. J. Stanley Gardiner, M.A. Reports: No. XIV. Marine Algae, Rhodophyceae. *Trans. Linn. Soc. Lond., 2nd Series, Zoology 16*: 269–306.

West, J.A., Zuccarello, G.C., Pedroche, F.F., Karsten, U. (1992). Marine red algae of the mangroves in Pacific Mexico and their polyol content. *Bot. Mar. 35*: 567–572.

Wynne, M. J. (1993). Benthic marine algae from the Maldives, Indian Ocean, collected during the R/V Te Vega Expedition. *Contr. Univ. Michigan Herb. 19*: 5–30.

Zuccarello, G.C., West, J.A., Kamiya, M. (2018). Non-monophyly of *Bostrychia simpliciuscula* (Ceramiales, Rhodophyta): Multiple species with very similar morphologies, a revised taxonomy of cryptic species. *Phycol. Res*. *66*: 100–107.

Figure captions

Figure 2. Number of benthic algal species, divided by major groups (Cyanobacteria, Phaeophyceae, Chlorophyta, Rhodophyta), reported from Central, Northern, and Southern Maldivian atolls.