Original Article

Spatio-temporal variation of macroalgal assemblages in southwestern Madagascar

Claudia Rodine[1]*, Henitsoa Jaonalison[4], Jean M. Kira[1], André Rakotoarimanana[2], Lantoasinoro N. Ranivoarivelo[1], Cicelin Rakotomahazo[1], Gildas B. G. Todinanahary[1], Gaëtan Tsiresy[3], Aina Le Don Nomenisoa[1], Fidèle Rakotonjanahary[1], Igor Eeckhaut[5], Mara E. Remanevy[1], Spencer Jamie[6], Richard Rasolofonirina[1], Thierry Lavitra[1]

[1] Institut Halieutique et des Sciences Marines (IH.SM), University of Toliara, 48B042 Rue Dr Rabesandratana HD, PO Box 141 - Toliara 601, Madagascar

[2] University of Toamasina, CUR Barikadimy, Building B, 4th, Toamasina 501, Madagascar

[3] University of Toamasina, ISTRCE, Box 60, Fénérive-EST 509, Madagascar.

[4] Laboratory of Evolutionary Ecology, FOCUS, University of Liège, B-4000 Liège, Belgium.

[5] University of Mons, 20 Place du Parc, 7000 Mons, Belgium.

[6] Feed-Back Madagascar NGO, Lot II M 98 i Antsakaviro, Antananarivo 101, Madagascar.

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*** Corresponding author:**
rodineclaudia@gmail.com

Abstract
The spatial and temporal distribution of macroalgal assemblages at 10 sites in the Baie de Ranobe and Baie de Toliara in southwestern Madagascar were investigated during warm (February to March) and cool (July to August) seasons. Algal species were identified and coverage estimated at six habitats between the shore and 15 m depth, based on surveys with 0.5 m x 0.5 m quadrats along transects of 30 m long by 5 m broad. Ninety eight taxa (53 red, 24 green, 21 brown) were identified of which 42 were edible. Species dominance varied by bay and season, with *Sargassum latifolium* dominating during the warm season, and *Hypnea musciformis* and *Ulva lactuca* prevalent during the cool season. Algal cover did not differ significantly between bays, but cover differed significantly between habitats. *S. latifolium*, *U. lactuca*, and *H. musciformis* were prominent on the algal shelf, *Ulva reticulata* on the inner shelf, and *Amansia rhodantha* on the outer shelf. Edible seaweed proportions increased during the cool season, particularly at algal and inner-shelf habitats. Generalized Linear Model analysis confirmed significant differences in edible algal cover across habitats and seasons. The potential of sustainably using macroalgae for aquaculture and human consumption in southwestern Madagascar is highlighted.

Keywords: species richness, species cover, edible seaweed, season, Ranobe Bay, Toliara Bay

Introduction
Madagascar, an island nation renowned for its extraordinary biodiversity and unique ecosystems, is situated in the Southwestern Indian Ocean off the coast of Africa. With an approximate land area of 587,041 Km^2, Madagascar boasts a coastline stretching over 5,603 km (Sanbar, 2015). Following its geographic isolation from Africa and India millions of years ago, Madagascar has evolved diverse flora and fauna species. Over 13,780 plant species and 2,108 animal species have been recorded, of which many are endemic to the island (CBD, 2024). Furthermore, the marine diversity surrounding Madagascar encompasses over 5,000 species, reflecting the island's ecological richness (MESUPRES, 2018).

However, despite its natural ecosystem richness, Madagascar faces significant socioeconomic challenges. The country is consistently ranked among the world's poorest, with high levels of hunger and malnutrition. According to the Global Hunger Index (GHI) ranking in 2022, Madagascar was placed as the 119th of 121 countries in the world, highlighting the severity of the nation's socioeconomic issues (Grebmer *et al.*, 2022). Malnutrition, particularly prevalent among children, remains a major challenge, with nearly half of children under the age of five suffering from stunting (Rakotomanana *et al.*, 2016). In addition, the majority of Madagascar's population lives in extreme poverty, earning less than 2 USD per day (Razakamanana *et al.*, 2023). This disastrous situation is underscored by a low Multidimensional Poverty Index (valued at 0.4), which places Madagascar among the bottom five countries in Sub-Saharan Africa (GMPI, 2023) and highlights the need for urgent intervention (UNDP, 2022).

The southern region of Madagascar, comprised of the administrative regions of Atsimo-Andrefana, Androy, and Anosy, known as the 'Grand Sud' or 'Deep South,' is particularly vulnerable to these socioeconomic issues. With a population of approximately 2.74 million (11 % of the nation's total population), the Deep South is one of the areas with the highest rates of poverty and food insecurity and most limited access to essential services (Harrington *et al.*, 2022). Ninety percent of the population lives below the poverty line (Harrington *et al.*, 2022). Key indicators of living conditions in the region, such as poverty rates and undernourishment, are significantly worse than the national average, exacerbating the challenges faced by its inhabitants (Healy, 2018; Gondard *et al.*, 2023). Recurrent droughts due to the arid climate further compound this situation, leading to crop failures and food crises (Ralambomanantsoa *et al.*, 2023). Recently, a severe food crisis has struck the region, causing tens of thousands to face famine-like conditions (Harrington *et al.*, 2022).

To help address these challenges, the 'Institut Halieutique et des Sciences Marine' of the university of Toliara (IH.SM), in collaboration with Feedback Madagascar and Mara Seaweed Company, has launched the Global Seaweed STAR project. This initiative aims to address food insecurity in Madagascar by harnessing the nutritional potential of seaweed.

Seaweeds, also known as macroalgae, are multicellular photoautotrophic organisms predominantly found in coastal and marine ecosystems. Classified into three major groups according to the nomenclature of Algae Base, Rhodophyta (red algae), Chlorophyta (green algae), and Heterokontophyta (brown algae, class Phaeophyceae) seaweeds offer rich nutritional benefits and serve as essential resources for various industries (Mohiuddin *et al.*, 2023). With approximately 12,000 species identified so far, including nearly 500 species collected from natural sources and used locally and about 33 genera commercially farmed, seaweeds represent a promising alternative food source rich in micro- and macro-nutrients, vitamins, and other essential compounds (Akrong *et al.*, 2021).

Today, seaweed cultivation has emerged as one of the world's fastest-growing industries, with nearly 130 countries engaging in farming or harvesting seaweeds on industrial or experimental scales (FAO, 2021). The total output of seaweed production has risen significantly over the years, highlighting the economic and nutritional importance of seaweed (FAO, 2021).

Despite Madagascar's rich biodiversity, documentation of its marine flora remains inadequate, with current estimates likely underestimating the true algal diversity (Vieira *et al.*, 2021). Consequently, the aim of this study was to assess the spatial and temporal variation of seaweed assemblages in the southwest of Madagascar. By evaluating the potential of seaweed as a sustainable food source to combat food insecurity and contribute to the valorization of Malagasy seaweed, this research seeks to address pressing socioeconomic and environmental challenges facing Madagascar's coastal communities.

Materials and methods

Study area

The study was conducted in Baie de Ranobe (BR) and Baie de Toliara (BT) (Fig. 1). BR is located between 23°3'0" S and 43°33'0" E, and is limited by the Manombo river in the north and by the Fiherenana river in the south. The BT, situated between 23°25'0" S and 43°42'0" E, is a small bay adjacent to BR. It is located between the Fiherenana river in the north and the Onilahy river in the south. These rivers play a crucial role in transporting substantial terrigenous inputs from their respective watersheds, making them the primary contributors to lagoon sedimentation. Moreover, they have a significant influence on seawater turbidity, particularly during the rainy season.

The coral reefs present in BR and BT are classified as continental outer barrier reefs. The choice of these two bays as study areas was based on the fact that their reefs exhibit distinct characteristics compared to the reefs located farther north and south of these bays, which are classified as complex coastal barrier reef complexes (Mahafina, 2011). Additionally, these areas have received considerable attention in research and tourism due to their biodiverse marine (coral reefs, seagrasses, and seaweeds) and coastal (mangrove) ecosystems.

Five monitoring sites were established in each bay. In BR, these sites were referred to as BR1, BR2, BR3, BR4, and BR5, while the sites in BT were labeled as BT1, BT2, BT3, BT4, and BT5 (Fig. 1).

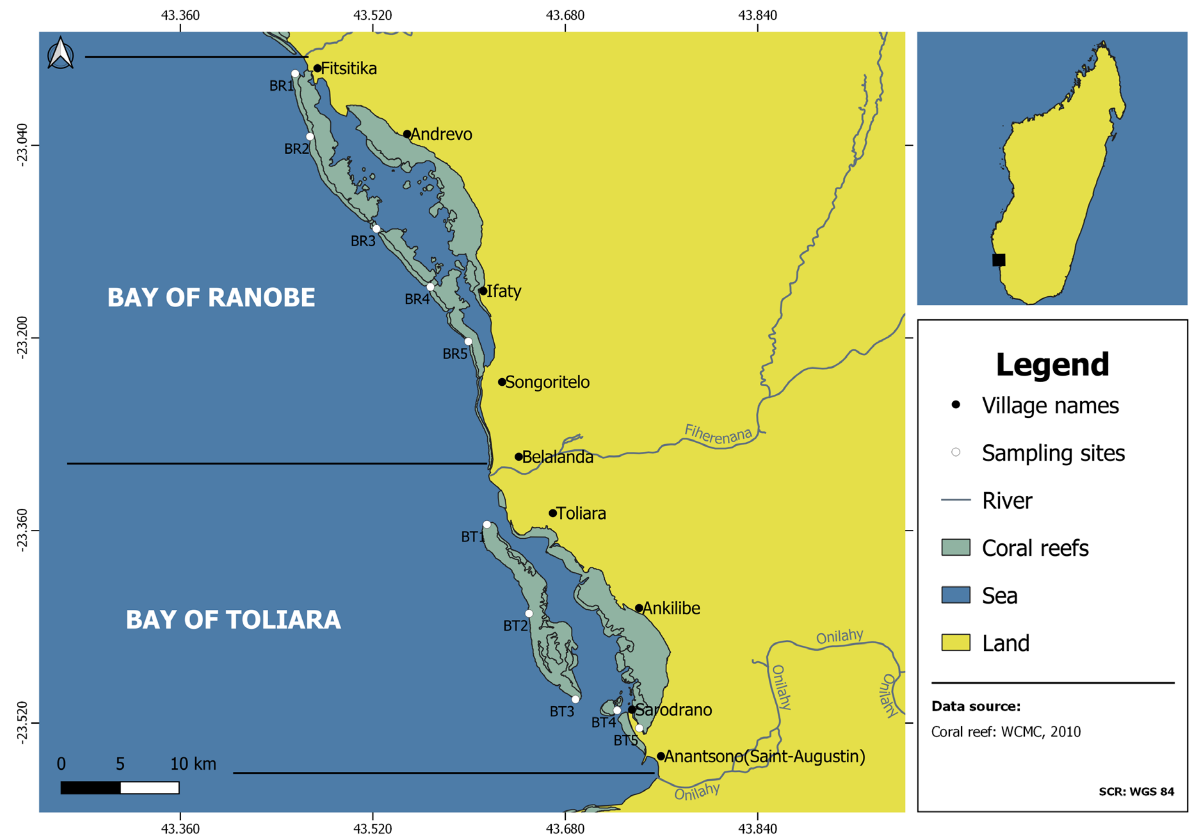

Figure 1. Location of the Baie de Ranobe and the Baie de Toliara and the studied sites.

Sample and data collection

The research was carried out during the warm season (February-March 2022) and the cool season (July-August 2022). Within each site, six habitats - littoral, inner-shelf, algal shelf and outer-shelf (0-5 m, 5-10 m and 10-15 m) - were surveyed. At each habitat, four transect lines (30 m), were haphazardly placed perpendicular to the waterline to inventory the macroalgae and to identify their distribution, with a minimum distance of 10 m between transects. Within each transect, the observation width extended to 2.5 m on both sides of the median line, giving an area of 150 m². Systematic identification of all encountered algae species within each transect was conducted. However, to estimate the percentage cover of algae species, six quadrats of 0.25 m² (0.5 m x 0.5 m) each were systematically positioned at 5 m intervals, altering between the left and right sides of the median line of the transect, from start to finish of the 30 m transect. Visual estimation and on-site scoring of the cover for each identified algal species within a quadrat were conducted, with cover recorded as rounded percentages based on visual observations. Additionally, each quadrat was photographed, serving as an observational and analytical reference for verification and further analysis. On-site identification of algae was performed macroscopically, primarily based on morphological characteristics. Uncommon specimens, not easily identifiable by divers, were initially photographed, carefully collected, and securely packaged for subsequent detailed examination in the laboratory. This approach allowed for more precise observations and analysis of these specimens. The algal identification process involved utilizing taxonomic keys (Richmond, 1997; Jha *et al.*, 2009; Pereira, 2016) and local checklists (Mollion, 2019; Vieira *et al.*, 2021) to determine the algae's taxonomic classification at the most specific level possible. The names of the identified species, along with their classifications, were cross-validated using AlgaeBase (www.algaebase.org), a trusted online resource for algae taxonomy and nomenclature.

The classification of species as edible was based on Pereira (2016), which provides insight into the functional uses of various algae.

At each site, in situ measurements of various parameters, including temperature, salinity, light, and pH, were conducted to characterize the environmental conditions. The mean salinity was 37.21 ± 1.61 psu, and the mean pH was 7.48 ± 0.07. Water temperature varied between 24.5 ± 1.25 °C (cool season) and 28.5 ± 0.51 °C (warm season), while luminosity ranged from 4,902 ± 6,181 lux (outer-shelf, 10-15 m) to 20,396 ± 36,690 lux (algal-shelf).

Data analysis

For marine macroalgae in general and edible species in particular, non-metric multidimensional scaling (nMDS) was used to visualize the spatial and temporal distribution of seaweed assemblages, i.e., between seasons (Cool and Warm), bays (BT and BR) and among habitats (Littoral, Inner-shelf, Algal-shelf, Outer-shelf 0-5 m, 5-10 m and 10-15 m). The eventual differences in macroalgal assemblages were then tested using the Analysis of Similarity (ANOSIM). When ANOSIM exhibited a significant difference, Similarity Percentage test (SIMPER) was performed to determine the taxa having the greatest contribution to the dissimilarity. Finally, Generalized Linear Model (GLM) was also used to examine differences in proportion of edible algae species among habitats. All the statistical analyses were performed with R software (version 4.2.1, R Core Team, 2021).

Results

Species richness

A total of 98 marine macroalgae taxa (53 red, 24 green and 21 brown) were observed in the coastal habitats of

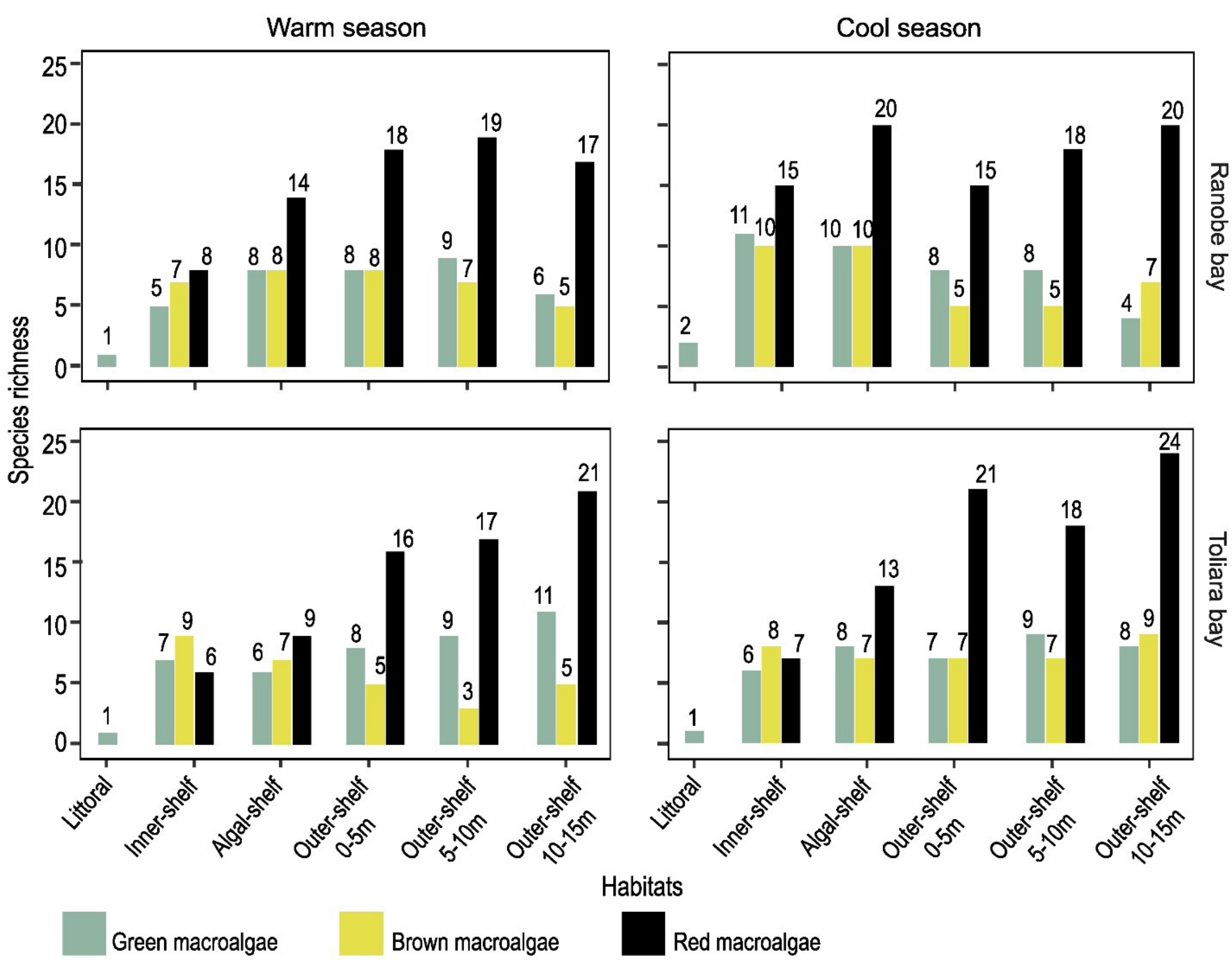

Figure 2. Spatial and seasonal distribution of algae species richness along the coastal habitats from the littoral to the reef outer-shelf at 15m depth.

Southwestern Madagascar, of which 42 are edible (16 red, 12 green and 14 brown) and 56 are not (37 red, 12 green and 7 brown, Table 1).

The species richness in terms of algae is higher in the Baie de Ranobe (89 taxa) than in the Baie de Toliara (80 taxa). The seaweed richness was spatially and seasonally dominated by the red algae (Fig. 2). Additionally, the cool season was richer in red algae species than the warm season. The highest species richness of red seaweed occurred in the algal shelf and outer-shelf, especially in the deepest outer-shelf (Fig. 2).

Table 1. Presence-Absence of algae species among habitats and seasons split by their use (edible or not) and the algae type (green, brown and red).

Color	Genus species	Seasons			Habitats					
		Edible	Cool	Warm	Littoral	inner-shelf	algal-shelf	Outer-shelf 0-5m	Outer-shelf 5-10m	Outer-shelf 10-15m
Red	*Acantophora spicifera*	Yes	1	1	0	1	1	0	0	0
	Amansia glomerata	Yes	1	0	0	1	1	1	1	1
	Amphiroa fragilissima	Yes	1	1	0	1	1	1	1	1
	Asparagopsis taxiformis	Yes	1	1	0	1	1	0	0	1
	Digenea simplex	Yes	1	1	0	1	1	0	1	1
	Euchema denticulatum	Yes	0	1	0	0	0	1	0	0
	Galaxaura rugosa	Yes	1	1	0	0	1	1	1	1
	Gelidiella acerosa	Yes	1	0	0	0	1	0	0	0
	Gracilaria corticata	Yes	1	1	0	1	1	1	1	1
	Gracilaria salicornia	Yes	1	1	0	1	1	1	1	1
	Halymenia durvillei	Yes	1	1	0	1	1	1	1	1
	Hypnea cervicornis	Yes	1	0	0	1	1	1	0	0
	Hypnea musciformis	Yes	1	1	0	1	1	1	1	1
	Hypnea pannosa	Yes	1	1	0	0	0	0	1	1
	Kappaphycus striatus	Yes	0	1	0	0	0	1	0	0
	Portieria hornemannii	Yes	1	1	0	0	0	1	1	0
Green	*Boodlea composita*	Yes	1	0	0	1	1	0	0	0
	Caulerpa laetevirens	Yes	1	0	0	0	1	0	0	0
	Caulerpa racemosa	Yes	1	1	0	1	1	1	1	1
	Codium arabicum	Yes	0	1	0	0	0	0	1	1
	Codium bursa	Yes	1	1	0	1	1	1	1	1
	Codium fragile	Yes	0	1	0	0	0	0	0	1
	Codium geppiorum	Yes	1	1	0	0	0	1	1	1
	Halimeda opuntia	Yes	1	1	0	1	1	1	1	1
	Ulva compressa	Yes	1	0	1	0	0	0	0	0
	Ulva intestinalis	Yes	1	1	1	1	1	0	0	0
	Ulva lactuca	Yes	1	1	0	1	1	1	1	1
	Ulva reticulata	Yes	1	1	0	1	1	1	1	1
Brown	*Colpomenia sinuosa*	Yes	1	0	0	1	1	0	1	1
	Dictyota dichotoma	Yes	1	1	0	1	1	1	1	1
	Dictyota friabilis	Yes	0	1	0	0	0	1	0	0
	Hormophysa cuneiformis	Yes	0	1	0	1	1	0	0	0
	Hydroclathrus clathratus	Yes	1	1	0	1	1	0	0	1
	Lobophora variegata	Yes	1	1	0	0	0	1	1	0
	Padina boryana	Yes	1	0	0	1	1	0	1	1
	Padina gymnospora	Yes	1	1	0	1	1	0	0	0
	Padina pavonica	Yes	1	1	0	1	1	1	1	1
	Sargassum crassifolium	Yes	1	1	0	0	0	1	1	1
	Sargassum ilicifolium	Yes	1	1	0	1	1	0	0	1
	Turbinaria conoides	Yes	1	1	0	1	0	1	0	0
	Turbinaria decurrens	Yes	1	1	0	1	1	1	1	1
	Turbinaria ornata	Yes	1	1	0	1	1	1	1	1

Color	Genus species		Seasons		Habitats					
		Edible	Cool	Warm	Littoral	inner-shelf	algal-shelf	Outer-shelf 0-5m	Outer-shelf 5-10m	Outer-shelf 10-15m
	Acantophora muscoides	No	1	0	0	0	1	0	0	0
	Actrinostrichia fragilis	No	1	0	0	1	1	0	0	0
	Amansia rhodantha	No	1	1	0	0	1	1	1	1
	Amphiroa anceps	No	1	1	0	1	1	1	1	1
	Amphiroa rigida	No	1	1	0	1	1	1	1	1
	Amphiroa sp1	No	1	0	0	0	0	0	0	1
	Amphiroa sp2	No	1	1	0	0	0	1	1	1
	Callithamnion stuposum	No	0	1	0	0	0	0	0	1
	Carpopeltis maillardii	No	0	1	0	0	0	1	0	1
	Cryptonemia natalensis	No	0	1	0	0	0	0	0	1
	Dasia stanleyi	No	1	1	0	0	0	1	1	1
	Dictyomenia sp	No	0	1	0	0	0	0	1	0
	Eucheuma platicladum	No	1	0	0	1	1	1	1	1
	Eucheuma sp	No	1	0	0	1	1	1	1	1
	Galaxaura obtusata	No	1	1	0	0	0	1	1	1
	Galaxaura tenera	No	1	1	0	1	1	1	1	1
	Galaxaura verprecula	No	1	0	0	1	1	0	0	0
	Gelidium pteridifolium	No	1	1	0	0	1	1	1	1
Red	*Gibsmithia hawaiensis*	No	0	1	0	0	0	0	0	1
	Gracilaria millardeti	No	0	1	0	0	0	0	1	0
	Hypnea sp	No	0	1	0	0	0	0	0	1
	Jania adhaerens	No	1	1	0	1	1	0	1	1
	Kappaphycus sp	No	1	1	0	1	1	1	1	1
	Laurencia complanata	No	0	1	0	0	0	1	1	1
	Laurencia filiformis	No	1	1	0	0	1	1	1	1
	Laurencia sp	No	1	0	0	0	1	0	0	0
	Liagora ceranoides	No	1	0	0	0	0	0	0	1
	Liagora divaricata	No	0	1	0	0	1	0	0	0
	Lithophyllum tortuosum	No	0	1	0	0	0	1	0	0
	Peysonnelia capensis	No	1	1	0	0	0	1	1	1
	Peysonnelia simulans	No	1	1	0	0	0	1	1	1
	Phacelocarpus neurymenioides	No	1	1	0	0	0	1	1	1
	Phacelocarpus tristichus	No	1	1	0	0	0	1	1	1
	Platysiphonia delicata	No	0	1	0	0	0	1	0	1
	Ptilophora sp	No	1	0	0	0	0	0	0	1
	Spyridia hypnoides	No	0	1	0	0	0	0	1	0
	Tricleocarpa fragilis	No	1	0	0	0	1	1	1	1
	Boengersenia forbessi	No	1	1	0	1	1	1	1	0
	Bryopsis myosuroides	No	0	1	0	0	0	0	0	1
	Chlorodesmis fastigiata	No	1	1	0	1	1	1	1	1
	Cladophora sp	No	1	0	0	1	1	0	0	0
	Dictyosphaeria cavernosa	No	1	1	0	1	1	1	1	1
Green	*Dictyosphaeria versluysii*	No	1	1	0	1	1	0	0	0
	Halimeda macroloba	No	1	1	0	1	1	1	1	1
	Halimeda tuna	No	1	0	0	0	0	1	1	1
	Monostroma obscurum	No	0	1	0	0	0	0	0	0
	Udotea sp	No	1	0	0	0	0	1	1	1
	Valonia fastigiata	No	1	1	0	0	1	1	1	1
	Ventricaria ventricosa	No	1	1	0	0	0	1	1	0
	Cystoseira myrica	No	0	1	0	1	1	0	0	0
	Desmia sp	No	1	0	0	1	0	0	0	0
	Dictyota humifusa	No	1	1	0	0	0	1	1	1
Brown	*Dictyota liturata*	No	0	1	0	0	0	0	1	0
	Sargassum densifolium	No	0	1	0	0	1	0	0	0
	Sargassum latifolium	No	1	1	0	1	1	1	1	1
	Stypopodium multipartitum	No	1	1	0	0	1	0	0	1

Species cover

The species with a cover of more than 6 % in both sites are presented in Figure 3 for each season. During the warm season, the species *Sargassum illicifolium*, *Sargassum latifolium* and *Hormohpysa cuneiformis* were dominant in BR (with cover more than 20 %) while *S. latifolium*, *Sargassum densifolium* and *Amansia rhodantha* were dominant in BT. The dominant species during the cool season in BR were *Ampiroa sp2*, *A. rhodantha* and *Ulva lactuca,* while those in BT were *Lobophora variegata*, *U. lactuca* and *Hypnea musciformis*. *S. latifolium* was dominant in both bays during the warm season while *U. lactuca* was dominant in both bays during the cool season.

Spatial and seasonal variation of seaweed coverage

The nMDS ordination showed that seaweed cover differs between the seasons (Fig. 4a). An ANOSIM test revealed a significant dissimilarity between seasons (R: 0.12; p-value = 0.001). A SIMPER test demonstrated that this significant seasonal distribution was due to the high cover of *S. latifolium* (40 %) during the warm season and *H. musciformis* (20 %) and *U. lactuca* (22 %) during the cool season (Table 2). The observed separation of the two groups of samples in the warm season may reflect site-specific environmental variations between the two bays, such as differences in local hydrodynamic conditions and nutrient availability, which could influence seaweed coverage. Although the nMDS showed a slight difference in algae cover between the two bays (Fig. 4b), no significant difference was observed using ANOSIM statistics ($p > 0.05$).

Seaweed cover differs significantly between habitats, particularly the algal shelf and inner-shelf habitats that were clearly separated from the others (Fig. 5) with an ANOSIM statistical R of 0.38 and a p-value of 0.001. The SIMPER test revealed that these differences were linked to the high cover of *S. latifolium*, *U. lactuca* and *H. musciformis* in the algal-shelf, the *Ulva reticulata* in the inner-shelf and the *A. rhodantha* in the outer-shelf from 0 - 15m (Table 3).

Proportion and cover distribution of edible algae species

Among the 42 edible algae species observed during this study, the most dominant (>5 % cover) 32 species

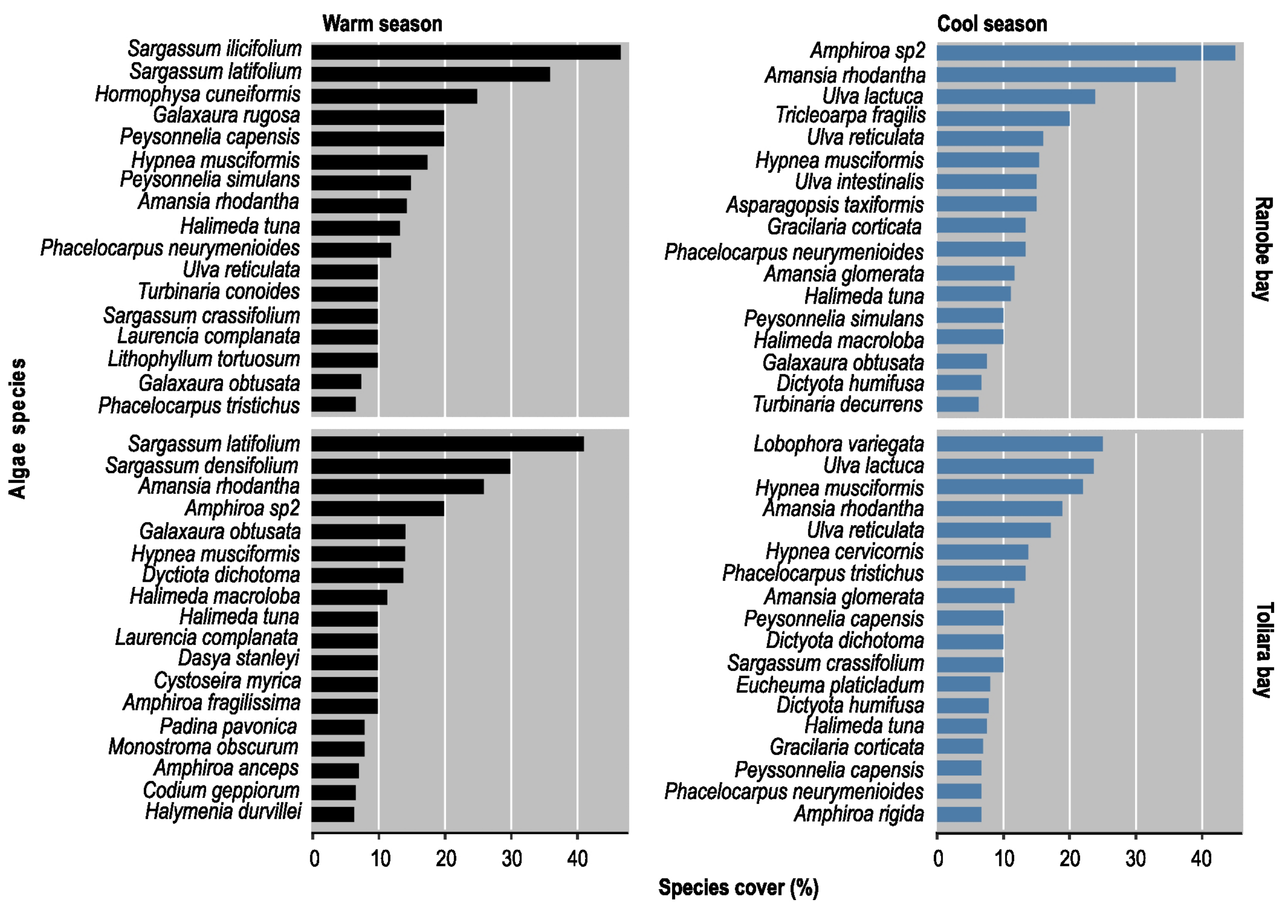

Figure 3. Species with a cover of more than 6 % in the two bays during warm and cool seasons.

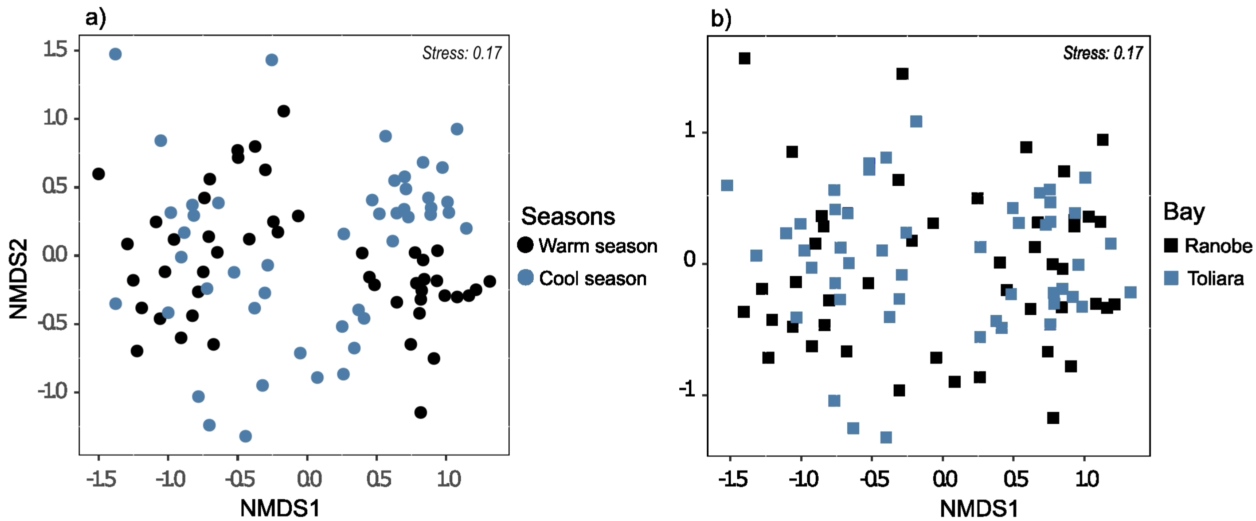

Figure 4. Seasonal distribution of seaweed cover through nMDS ordination; a) between seasons and b) between bays.

in BR and BT during the warm and cool seasons are presented in Figure 6. Dominance of edible species varies between the two bays and seasons. During the warm season, three species including *S. illicifolium, H. cuneiformis and Galaxaura rugosa* were most dominant in BR (>20 % cover) while *H. musciformis, Dictyota dichotoma*, and *Amphiroa fragilissima* are dominant in BT (>10 % cover). During the cool season, *U. lcatuca, U. reticulata and H. musciformis* were observed to be dominant in BR (>15 %) while *L. variegata*, *U. lactuca and H. musciformis* dominate in BT (>20 %). Seven species including *H. musciformis*, *U. reticulata*, *Halimeda opuntia*, *Turbinaria decurrens*, *Padina pavonica*, *Gracilaria corticata*, and *U. lactuca* were observed during the two seasons in both bays (Fig. 6).

The findings exhibit that the proportion of edible seaweed species was extremely important during the cool season. The highest proportion values during the cool season were found in the algal-shelf and inner-shelf (Fig. 7), in which more than 75 % of the recorded marine algae were edible species. Such a pattern has been observed in both the BR and BT and for all the studied sites in each bay. The Generalized-Linear Model (GLM) showed that the proportion cover of edible algae in the algal-shelf and inner-shelf differs significantly from other habitats with respective p-values of 0.049 and 0.02. On the outer-shelf, the marine algae comprised around 50 % of edible species.

The cover of edible marine algae also differed significantly between the warm and cool season (ANOSIM statistic R = 0.10, p-value = 0.001). SIMPER revealed that this difference is due to the high cover of *H. musciformis* and *U. lactuca* occurring during the cool season (Table 4). The cover of edible marine algae also significantly differed between the two bays and between different habitats, with p-values of 0.02 and 0.001 respectively. However, the ANOSIM statistic R was very low for the difference between bays (R=0.05)

Table 2. Top 10 discriminating species for each season (i.e., characteristic of each season).

Rank	Species	Warm season	Cool season	Cumulated contributions
1	*Sargassum latifolium*	0.15	0.01	8.9
2	*Hypnea musciformis*	0.10	0.14	17.6
3	*Amansia rhodantha*	0.10	0.08	25.6
4	*Ulva lactuca*	0.01	0.12	32.8
5	*Ulva reticulata*	0.02	0.06	37.0
6	*Dictyota dichotoma*	0.04	0.05	41.0
7	*Halimeda macroloba*	0.05	0.02	44.2
8	*Halimeda tuna*	0.02	0.04	47.1
9	*Galaxaura obtusata*	0.04	0.01	49.9
10	*Gracilaria corticata*	0.02	0.04	52.7

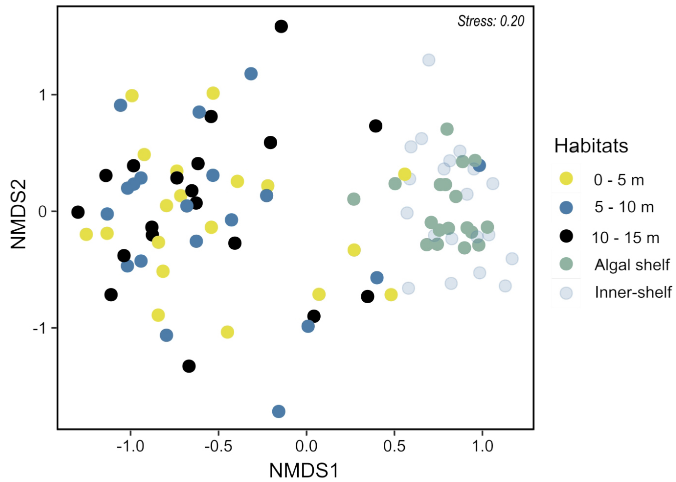

Figure 5. Ordination of the cover distribution of seaweed according to different habitats using nMDS.

while it was high among habitats (R=0.28). Based on SIMPER results, the difference in edible algae cover between habitats was mostly due to the high coverage of *H. musciformis* and *U. lactuca* on the algal shelf, *U. reticulata* on the inner-shelf, and *Dictyota dichotoma* on the outer-shelf between 5 – 15 m (Table 5).

Discussion

Seaweed species richness: Contrasting Southwest Madagascar with national diversity

In this study, 98 marine algae taxa were identified in the Southwestern region of Madagascar, consisting of 53 red, 24 green, and 21 brown species. In contrast, Mollion (2019) documented 69 species within the same Southwestern region, which included 35 red, 18 green and 16 brown species. The present study discovered additional 29 species comprising 18 red, 6 green and 5 brown likely due to a more comprehensive sampling approach. Mollion's study focused only on the fringing and barrier reefs without specifying the sampling period, while the current study covered a broader range of morphological areas and depths. These included the survey of the littoral, inner-shelf, algal shelf, and outer-shelf (0-5 m, 5-10 m, and 10-15 m) areas across the two bays, covering two distinct seasons. Furthermore, while Mollion identified a total of 92 species across multiple regions of Madagascar—including the Southwestern, Southern, Southeastern, and Northeastern regions, such as Saint Marie —the findings reported on here specifically reflect the diversity present in the Southwestern region alone. In contrast, Vieira *et al.* (2021) reported a total of 442 algae species in Madagascar, with 241 red, 116 green, and 85 brown algae. This national dataset highlights significant variations in seaweed distribution across different regions of Madagascar, underscoring the complexities of marine biodiversity that cannot be fully captured in localized studies alone. As an example, Mollion (2019) recorded 16 species in the Southern and Southeastern regions of Madagascar that this study did not identify in the Southwestern region. These include three species of green algae (*Bryopsis sp*, *Caulerpa taxifolia* and *Codium duthiae*), two species of brown algae (*Ecklonia sp* and *Stypopodium sp*) and 11 species of red algae (*Botryocladia madagascarensis*, *Cryptonemia. sp*, *Gelidium madagascariense*, *Gracilaria mamillaris*, *Martensia elegans*, *Plocamium sp*, *Porphyra sp*, *Sarconema filiforme*, *Solieria sp*, *Solieria robusta* and *Yoganugia ligulatus*). Moreover, the current study revealed 27 species that were not mentioned in the study by Vieira *et al.* (2021), comprising

Table 3. The characteristic species contributing to the difference between habitats from a SIMPER test.

Rank	Species	Algal-shelf	Inner-shelf	Outer-shelf		
				0 – 5m	5 – 10m	10 – 15m
1	*Sargassum latifolium*	0.17	0.16	0.02	0.03	0.01
2	*Ulva lactuca*	0.19	0.13	0.01	0.01	0.01
3	*Hypnea musciformis*	0.26	0.20	0.06	0.06	0.04
4	*Ulva reticulata*	0.06	0.12	0.01	0.01	0.01
5	*Amansia rhodantha*	0.01	0.00	0.16	0.13	0.15

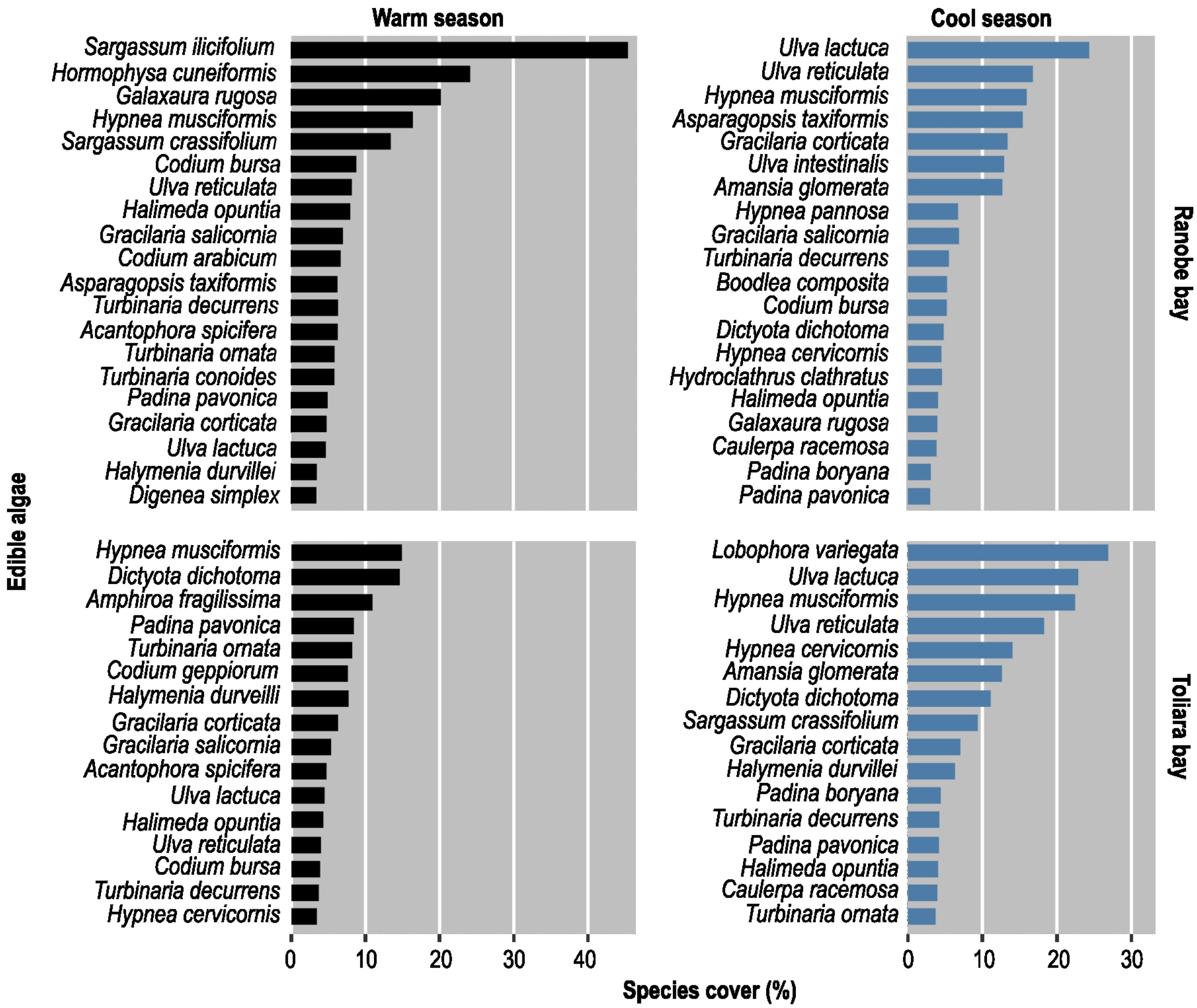

Figure 6. Dominant edible algae species (>5 %) in the BR and BT during the warm and cool seasons.

18 red, 6 green, and 3 brown algae. This divergence highlights the importance of localized studies in capturing region-specific biodiversity, as well as the need for continued research to fully catalog and understand the marine flora of Madagascar. It is noted that among the 27 species that were not reported by Vieira *et al.*, 2021, 16 were already reported in the Indian Ocean Islands and 10 were observed in African countries.

Comparison of seaweed species richness: Madagascar and continental East Africa

In this section, the seaweed species richness of Madagascar with that of continental East Africa is compared, highlighting the significant biodiversity present in these regions. The 98 species identified in the present study contribute to the overall biodiversity of Madagascar's marine flora. Vieira *et al.* (2021) reported a total of 442 algae species in Madagascar, comprising 241 red, 116 green, and 85 brown algae. This species richness highlights an important aspect of Madagascar's unique marine ecosystems, although true biodiversity also encompasses factors such as species distribution and genetic variation.

According to AlgaeBase, Madagascar has a total of 606 recorded seaweed species. In comparison, Kenya has 875 species, Tanzania has 583 species, and Mozambique has 652 species (Guiry and Guiry, 2024). These figures illustrate the considerable diversity present along the African coast, which encompass distinct biogeographical regions characterized by unique seaweed communities (Bolton *et al.*, 2003).

Overall, Africa hosts a total of 8,886 recorded seaweed species, with the Indian Ocean Islands accounting for 1,583 species. These comparisons emphasize the need for localized studies to understand the ecological dynamics and species distributions in Madagascar's marine environments.

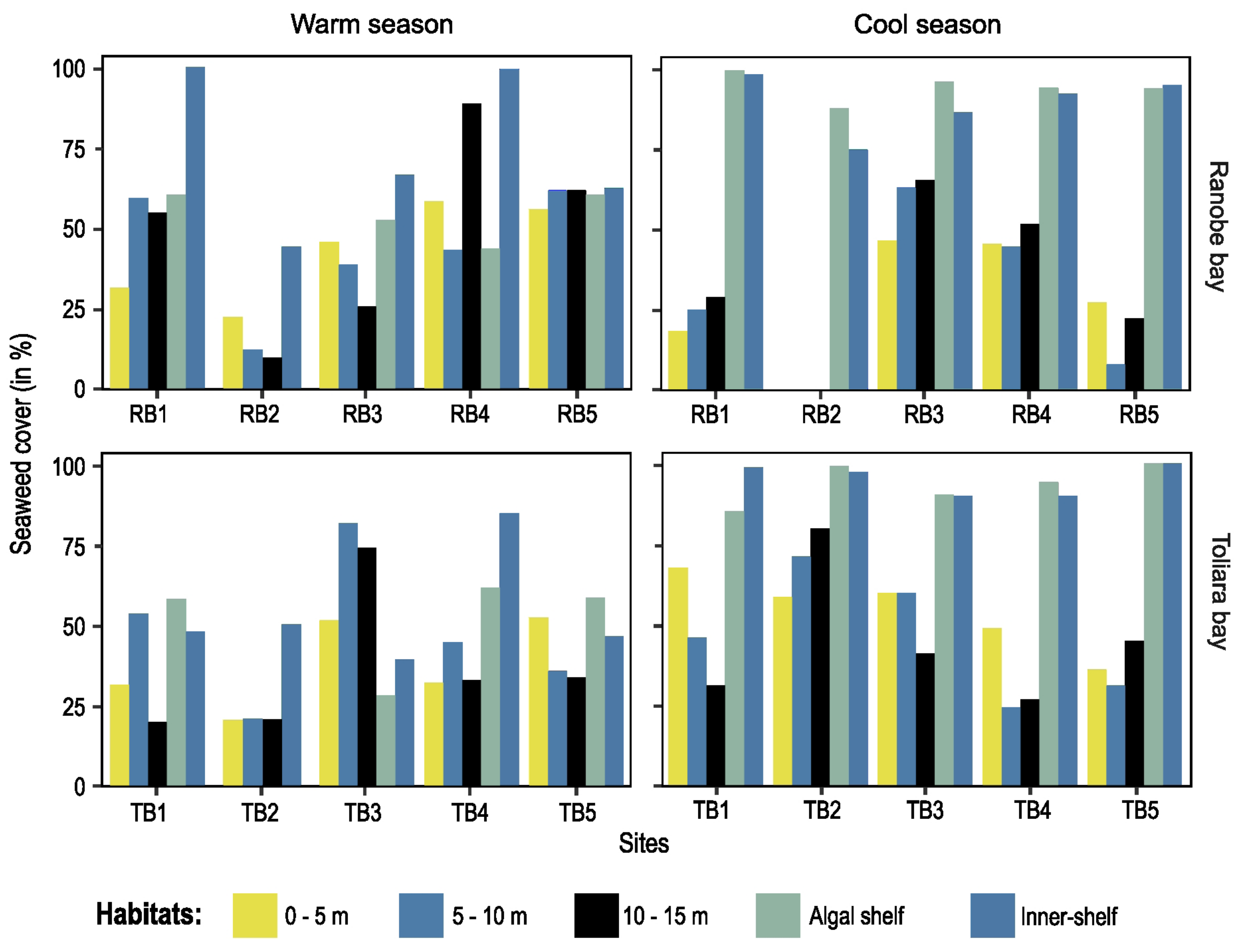

Figure 7. Spatial and seasonal variation in the proportion of edible marine algae.

Species richness among the three groups (red, green and brown)

This study highlighted that red algae are significantly richer in species compared to green and brown algae. This finding aligns with the species richness observed at the national level (Vieira *et al.*, 2021) and is consistent with results from various studies, except for that of Mushlilah *et al.*, 2021. Rhodophytes (red algae) are characteristically diverse and abundant in both tropical and temperate regions (Littler and Littler, 2003) exhibiting a wider ecological amplitude compared to the other two seaweed groups (Romdoni *et al.*, 2018).

Typically, species richness of red algae is followed by the green algae and then brown algae, as seen in the results of this study. A similar trend has been reported by authors in different regions including South Africa (Bolton *et al.*, 2003), Ghana (Akrong *et al.*, 2021), NE and SE Brazil (Cavalcanti *et al.*, 2022), Atol das Rocas, Brazil (Villaça, 2010), the eastern coasts of Qeshm Island, Persian Gulf, Iran (Kobabi *et al.*, 2016), Vietnam (Nguyen *et al.*, 2013), Myanmar (Soe-Htun, 2010) and The Pari Island Reef Cluster, Jakarta, Indonesia (Zulpikar *et al.*, 2020). However, species richness of green algae is sometimes less than that of brown algae,

Table 4. Edible species contributing to the difference between seasons using the SIMPER test.

Rank	Species	Warm season	Cool season	Cumulated contributions
1	*Hypnea musciformis*	0.10	0.14	16.1
2	*Ulva lactuca*	0.01	0.12	28.0
3	*Dictyota dichotoma*	0.04	0.05	36.8
4	*Ulva reticulata*	0.02	0.06	43.8
5	*Padina pavonica*	0.05	0.01	49.3

Table 5. Edible species contributing to the difference between habitats using the SIMPER test.

Rank	Genus species	Algal-shelf	Inner-shelf	Outer-shelf		
				0 – 5m	5 – 10m	10 – 15m
1	*Hypnea musciformis*	0.26	0.20	0.06	0.06	0.04
2	*Ulva lactuca*	0.19	0.13	0.01	0.01	0.01
3	*Ulva reticulata*	0.06	0.12	0.01	0.01	0.01
4	*Dictyota dichotoma*	0.02	0.01	0.04	0.08	0.07

as reported in other studies like in Udo, Jeju Island in Korea (Kang *et al.*, 2011), Sao Miguel, in the Azores archipelago, Portugal (Neto, 2001) and the Persian Gulf (Niamaindi *et al.*, 2017).

To explore these patterns further, the Cheney ratio (R+G)/B was calculated, where R represents the number of red algae species, G the number of green algae species, and B the number of brown algae species. This study found a Cheney ratio of 3.66 in Southeastern Madagascar, which is slightly lower than the 4.2 reported by Vieira *et al.* (2021) for Madagascar as a whole. In comparison, Phu Yen Province in Vietnam reported a Cheney ratio of 3 (Hang *et al.*, 2020), while a notably high ratio of 23.6 was documented in Campeche, Mexico (Hernández-Casas *et al.*, 2024). The high Cheney index value observed in Campeche indicates a tropical affinity of its flora, as values greater than six signify tropical characteristics.

Biogeographic affinity can also be inferred from the Cheney index values. For instance, estuaries and coastal flora in Campeche exhibit Cheney indices between 6.5 and 13, further supporting their classification as tropical flora. In contrast, lower values found in the Northwest Atlantic—where ratios vary from 1.0 in Churchill, Hudson Bay (Saunders and McDevit, 2013) to 5.9 in tropical waters of Florida (Dawes and Mathieson, 2008)—indicate a transition to temperate affinities.

These comparisons illustrate the considerable diversity present along African coastlines and underscore the varying ecological dynamics and species distributions across different marine environments. Understanding these patterns provides valuable insights into the ecological dynamics of seaweed communities, particularly regarding biogeographic affinities and the importance of localized studies in characterizing marine biodiversity.

Spatial and seasonal variation of species richness

This research has revealed that the dominance of seaweed varies according to the season, bay, site, and habitat. This finding aligns with other ecological studies (Raffo *et al.*, 2014; Kobabi *et al.*, 2016; Melsasail *et al.*, 2018), which have shown that the structure and composition of macroalgal assemblages fluctuate both temporally and spatially due to seasonal variations in rainfall, salinity, nutrients, and light intensity (Kobabi *et al.*, 2016). According to Mushlilah *et al.* (2021), the distribution of macroalgae is influenced by various environmental factors, ranging from anthropogenic pressures such as the activities of local communities and tourists to the environmental parameters of the waters. Environmental parameters include wave action, substrate, and nutrients (Thakur *et al.*, 2008; Kang *et al.*, 2011; Petsut *et al.*, 2012). Dıez *et al.* (2003) have also noted that abiotic factors such as substratum, nutrients, water motion, sedimentation and pollution affect the structure and distribution of algal communities at a local scale. However, seawater temperature is considered one of the important physical factors determining seaweed distribution (Zhuang and Zhang, 2001).

The succession of seaweed assemblages over time may be attributed to the seasonal fluctuation of nutrient supplies in seawater in the study area (Kobabi *et al.*, 2016). In the present study, the dominance of Ulva species (*U. lactuca* and *U. reticulata*) was observed during the cool season and the dominance of Sargassum species during the warm season. Phillips and Hurd (2003) have reported that Ulva species are among the fast-growing algae and exhibit temporal differences, being abundant in winter and early spring but diminishing in summer (Kobabi *et al.*, 2016). However, the strategies of annual seaweeds that develop during late spring to summer in periods of low nutrient supplies, such as Sargassum species, are poorly investigated (Vaz-Pinto *et al.*, 2014). It is possible that these Sargassum species exhibit slow-growing perennial characteristics, similar to other perennial seaweeds, with low nutrient uptake rates. According to Kobabi *et al.* (2016), slow-growing perennials accumulate large nutrient pools in winter, which support their growth in spring/summer when light levels increase. While specific studies on Sargassum nutrient uptake strategies are limited, this general pattern may explain their dominance during the warm season in the current study.

Potential of seaweed for aquaculture and human consumption

During this study, seven dominant seaweed species with significant potential for aquaculture and consumption were consistently observed across the two bays (BR and BT) during the two seasons: *H. musciformis*, *U. reticulata*, *H. opuntia*, *T. decurrens*, *P. pavonica*, *Gracilaria corticata*, and *U. lactuca*. These species hold valuable nutritional properties that could address key food challenges in the southwestern part of Madagascar, a region known for its issues with food insecurity and malnutrition.

Among the species identified, *H. opuntia*, *T. decurrens*, and *P. pavonica* have been relatively underexplored in terms of large-scale farming. However, these species are rich in bioactive compounds and nutrients that are particularly beneficial in addressing dietary deficiencies. For example, *H. opuntia* has shown potential for use in enhancing human health, particularly due to its antioxidant properties, which can help protect cells from damage. Additionally, its antibacterial and antimicrobial qualities suggest its utility in promoting both human and aquaculture health (Nazarudina *et al*., 2022; Darfia *et al*., 2021; Radhika *et al*., 2022).

T. decurrens and *P. pavonica* are similarly promising. *T. decurrens* contains compounds with anticoagulant and anticancer properties, which could offer medicinal benefits alongside its nutritional potential (Shanthi *et al*., 2021; Sami and Nur, 2022). Moreover, it has shown efficacy in agricultural applications, such as controlling bacterial brown rot disease (Abd-El-Aziz, 2020), making it a candidate for addressing both health and agricultural productivity issues. *P. pavonica* has been studied extensively as a dietary supplement in fish aquaculture, with positive effects on growth and health, particularly for rabbitfish and Nile tilapia (Monier *et al*., 2022; Maghawri *et al*., 2023). Its consumption is considered safe due to its non-genotoxic and antioxidant properties (Güner, 2021), and its mineral content makes it a valuable nutritional addition to local diets.

U. reticulata, although less studied in terms of aquaculture trials, stands out for its medicinal and nutritional properties. It is rich in proteins, minerals, and iodine, making it a valuable food source for combating malnutrition, especially in regions where iodine deficiency is prevalent (Ratana-arporn and Chirapart, 2006). Its potential for managing diabetes, thanks to its ability to inhibit carbohydrate-metabolizing enzymes and promote insulin secretion, further highlights its value in addressing non-communicable diseases that may affect the population (Unnikrishnan *et al*., 2022).

The more widely cultivated species, such as *U. lactuca*, *H. musciformis*, and *G. corticata*, also demonstrate considerable nutritional potential. *U. lactuca* is rich in Ulvan, a polysaccharide known for its health benefits, including its ability to support immune function and reduce inflammation (Pappou *et al*., 2022; Dominguez and Loret, 2019). This species, already grown in various countries, could play a pivotal role in enhancing local diets by providing essential vitamins and minerals.

Similarly, *G. corticata* is recognized as a potential functional food due to its nutrient content, including essential fatty acids and proteins (Rosemary *et al*., 2019). The development of its cultivation could directly contribute to addressing protein shortages in the local population. *H. musciformis*, though lower in protein and carbohydrate content, is rich in essential minerals such as calcium, magnesium, sodium, and potassium (Balamurughan *et al*., 2013), which are vital for maintaining proper bodily functions and could help alleviate common mineral deficiencies in southern Madagascar.

In conclusion, the findings underscore the substantial nutritional potential of the identified seaweed species in the southwestern region of Madagascar. By promoting the cultivation and consumption of these species, local food challenges, including malnutrition and nutrient deficiencies, can be addressed. Further research and targeted cultivation efforts will be crucial for integrating these species into sustainable aquaculture systems and enhancing food security in the region.

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