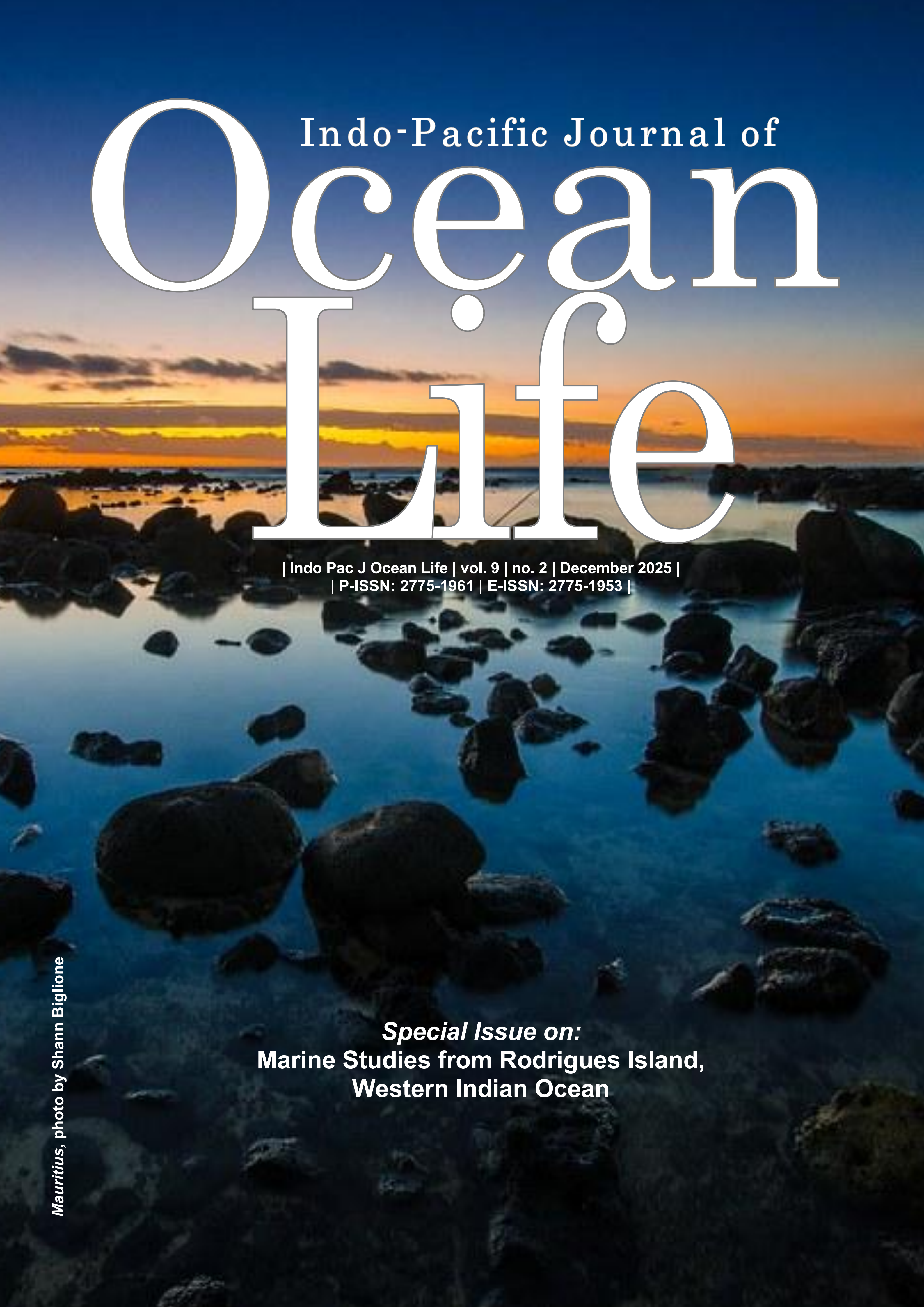

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The usage of "et al." in long author lists will also be accepted:

Smith J, Jones M Jr, Houghton L et al. 1999. Future of health insurance. N Engl J Med 965: 325-329. DOI: 10.10007/s002149800025.

Book:

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Chapter in the book:

Webb CO, Cannon CH, Davies SJ. 2008. Ecological organization, biogeography, and the phylogenetic structure of rainforest tree communities. In: Carson W, Schnitzer S (eds.). Tropical Forest Community Ecology. Wiley-Blackwell, New York.

Abstract:

Assaeed AM. 2007. Seed production and dispersal of *Rhazya stricta*. 50th annual symposium of the International Association for Vegetation Science, Swansea, UK, 23-27 July 2007.

Proceeding:

Alikodra HS. 2000. Biodiversity for development of local autonomous government. In: Setyawan AD, Sutarno (eds.). Toward Mount Lawu National Park; Proceeding of National Seminary and Workshop on Biodiversity Conservation to Protect and Save Germplasm in Java Island. Universitas Sebelas Maret, Surakarta, 17-20 July 2000. [Indonesian]

Thesis, Dissertation:

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Information from the internet:

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EDITORIAL NOTE
For Special Issue on

"Marine Studies from Rodrigues Island, Western Indian Ocean"

Indo-Pacific Journal of Ocean Life vol. 9, no. 2, December 2025

Greetings!

This special edition of "Marine Studies from Rodrigues Island, Western Indian Ocean" in the Indo-Pacific Journal of Ocean Life is dedicated to the late Dr. Ricardo F. Tapilatu from the Pacific Marine Resources Research Center, University of Papua (UNIPA), Manokwari, Indonesia, and the former Editor-in-Chief. The Editorial team of the Indo-Pacific Journal of Ocean Life received the request in September 2024, and the Editorial Office dedicated this special edition for the publication as volume 9 No. 2 in December 2025.

The researchers and students, including local and international ones, prepared the manuscripts under the Pole of Research Excellence in Sustainable Marine Biodiversity (PRE-SMB), led by Professor Ranjeet Bhagooli and the Department of Biosciences and Ocean Studies at the Faculty of Science of the University of Mauritius. As per the journal's requirements, several manuscripts falling under this special edition topic from the waters of Rodrigues were submitted. Following the standard peer-review process of the journal, accepted papers are presented in the special edition entitled "Marine Studies from Rodrigues Island, Western Indian Ocean." This special edition is published in the context that the coral reefs around Rodrigues Island harbors a relatively high marine biodiversity as part of the Republic of Mauritius in the western Indian Ocean. Coral reefs provide substantial ecological goods and services to the national economies of small island developing states supporting coastal communities. However, such ecosystems are under peril due to rapid climate change and anthropogenic disturbances.

This special edition entails marine studies around Rodrigues Island which is occupied by less than 45,000 inhabitants, and has a land area of 104 km^2, lagoon area of 300 km^2 and fringing reef of 200 km^2. Rodrigues Island form part of the Republic of Mauritius in the western Indian Ocean region. Though the Islanders from Rodrigues depend extensively on the marine ecosystems and associated resources very little is known and published about their marine ecosystems. This special issue adds to the existing scientific literature to further help sustainable use of the ocean resources and foster appropriate conservation and management measures in an era of a rapidly warming ocean.

This special edition presents original articles documenting several ecological studies along with some experimental investigations. The original paper by Ricot et al. assessed the herbivorous fish biomass at five sites around Rodrigues Island and found higher biomass in coral-dominated than the non-coral-dominated habitats Herbivorous fish has a pivotal role in maintaining coral recovery and resilience through control of macroalgal growth. Priest et al. documented the spatio-temporal density distribution of the crown-of-thorns (COTS) sea star (*Acanthaster*) and marine grastropod (*Drupella*) predation on corals. This study informed that *Drupella cornus*, rather than *Acanthaster* possibly represents a potential issue to reefs in Rodrigues. Jogee et al. investigated photosynthetic health performance of photosynthate producing dinoflagellate endosymbionts (Symbiodiniaceae) in four reef-building coral genera (*Montipora*, *Platygyra*, *Acropora*, *Favia*) affected by four coral diseases namely Black Band Disease (BBD), Skeletal Eroding Band (SEB), White Band (WS), and White Syndrome (WS), which tend to be increasing in prevalence and accelerating reef decline worldwide under climate change- and anthropogenically-driven impacts. Two of the studied coral diseases namely BBD and SEB had significant impacts on the photosynthetic functioning in two coral genera, *Montipora* and *Favia*, respectively. Jeetun et al. explored the thermal photosynthetic functioning of shaded- and light-exposed coral *Echinopora forskaliana*, which tended to exhibit bleaching in light-exposed conditions in the field. When subjected to thermal stress trials at a moderate light level, those from the exposed environments exhibited reduced photosynthetic performance and bleaching, implying shaded habitats as climate refugia and potentially useful in adaptive conservation and management approaches in a warning marine environment. Gerzer et al. documented a high-density aggregation of the sea cumcumber *Holothuria cinerascens* compared to *Holothuria atra* and *Stichopus horrens* in a limestone structural complex habitat providing a variety of crevices, appropriate water flow, predatory refugia and opportunities for attachment in a lagoon system of Rodrigues Island. Thorough understanding of holothurian ecology has implications for appropriate conservation and mariculture strategies. Mattapullut et al. presented the first record of *Annella mollis,* a gorgonian soft coral (Octocorallia) commonly called giant sea fan, at two outer reef slope sites namely Tombant Coco and Ti Paté at approximately 27 m deep from the waters of Rodrigues Island. Munbodhe and Bhagooli reported on the corals and reef fishes of Rodrigues Island with implications for regionally endemic species in a warming ocean. The endemic reef fish to Rodrigues, *Pomacentrus rodriguensis*, were observed both in marine protected and non-protected areas. The regionally endemic and rare reef fishes namely *Stegastes pelicieri*, *Stegastes limbatus*, *Pomacentrus pikei*, *Amphiprion latifasciatus*, and *Amphiprion chrysogaster* were sporadically observed in non-protected sites. Two regionally endemic corals *Acropora branchi* and *Pocillopora indiania*, were observed at all studied marine protected sites. Understanding the distribution of endemic and rare corals and reef fishes around Rodrigues Island is imperative for an enhanced protection and conservation strategy. Ramkalam et al. explored the distribution of soft corals and photo-physiology of bleached and non-bleached *Sarcophyton* sp. around Rodrigues. This study indicated dominance of some soft coral species at some of the studied sites and reduced photosynthetic performance in bleached compared to non-bleached *Sarcophyton*. Ramah et al. studied the changes in densities of two species of *Tridacna* over a decade at two protected areas of Rodrigues Island. The South East Marine Protected Area consistently supported higher densities, underscoring its role as a key refuge, while the English Bay Marine Reserve had lower densities for both species and limited recovery potential and thus indicating site- and species-specific variations in *Tridacna* densities.

The contributions of papers presented in this special edition bring forward new scientific information on marine diversity and distribution of key marine organisms and bleaching patterns of a reef-building coral from the coral reefs of Rodrigues Island. These findings may further inform appropriate protection and conservation related decision-making for an enhanced and adaptive management strategy for the coral reefs of Rodrigues Island in the western Indian ocean.

Professor (Dr) Ranjeet Bhagooli
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Herbivorous fish biomass and benthic composition around Rodrigues Island, Western Indian Ocean

MELANIE RICOT[1,♥], SRUTI JEETUN[1], SHAKEEL YAVAN JOGEE[1], MARWYN ANASAMY[1], DEEPEEKA KAULLYSING[1,2], NAWSHEEN TALEB-HOSSENKHAN[1], RANJEET BHAGOOLI[1,2,3,4,5,6]

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Abstract. *Ricot M, Jeetun S, Jogee SY, Anasamy M, Kaullysing D, Taleb-Hossenkhan N, Bhagooli R. 2025. Herbivorous fish biomass and benthic composition around Rodrigues Island, Western Indian Ocean. Indo Pac J Ocean Life 9: 81-91.* Herbivorous reef fish play a critical role in maintaining coral reef resilience by controlling algal growth and facilitating coral recovery. This study assessed the biomass of herbivorous fish and benthic composition across coral-dominated (high live hard coral cover >20%) and non-coral-dominated (low live hard coral cover <20%) habitats at five sites, namely, Aquarium, Plateau Bénitier, Ti Trou, Antonio's Finger, and Couzoupa around Rodrigues Island, Western Indian Ocean. Fish biomass was estimated using triplicate belt transects, focusing on key herbivorous families (Acanthuridae and Scaridae), while benthic composition was quantified to identify habitat-specific patterns. Results revealed higher herbivorous fish biomass in coral-dominated habitats (1028.54±847.78 kg/ha) compared to non-coral-dominated habitats (728.34±229.36 kg/ha). No significant differences ($p>0.05$) were observed in the biomass of the Acanthuridae ($p=0.56$) nor Scaridae ($p=0.36$) fish families between coral-dominated and non-coral-dominated habitats. Coral-dominated habitats exhibited higher live hard coral cover (64.03±9.55%) compared to non-coral-dominated habitats (7.3±1.32%). Additionally, a significant interaction between protection status and live coral cover was observed, indicating that both protection measures and coral cover levels jointly influence herbivorous fish biomass. These findings underscore the importance of benthic habitat structure, particularly coral cover, in shaping herbivorous fish communities and supporting higher fish biomass in coral-dominated habitats.

Keywords: Coral reef, functional groups, marine protected areas, reef fish, reef fish assemblages, reef resilience, tropical islands

Abbreviations: CCA: Canonical Correspondence Analysis, WIO: Western Indian Ocean

INTRODUCTION

Coral reefs are among the most biodiverse and productive ecosystems on Earth (Singh et al. 2022; Sobha et al. 2023). They provide numerous ecosystem services that are essential for human well-being (MEA 2005; Woodhead et al. 2019; Hafezi et al. 2021; Santavy et al. 2021; Sing Wong et al. 2022). However, coral reefs face growing threats from human activities, including overfishing, pollution, and the impacts of climate change, all of which are changing species composition and altering fundamental ecological processes (Mora et al. 2011; Hughes et al. 2017; Williams and Graham 2019; Obura et al. 2022).

Herbivorous fish play an essential role in maintaining coral reef health by regulating critical ecological processes (Green and Bellwood 2009; Adam et al. 2015a; Dromard et al. 2015; Fong et al. 2018; Robinson et al. 2018; Donovan et al. 2023; Sheppard et al. 2023). Their abundance, size, and feeding behavior make them significant contributors to the stability of coral reef ecosystems (Bellwood et al. 2004; Hughes et al. 2007; Bosch et al. 2022; Kindinger et al. 2024). They help control the growth of benthic algae, mediating competition between algae and scleractinian corals for reef space (Mumby et al. 2006; Hughes et al. 2007; Knoester et al. 2023; Sheppard et al. 2023), thereby promoting coral resilience and preventing shifts to less resilient states (Mumby et al. 2006; Hughes et al. 2007; Holbrook et al. 2016; Nash et al. 2016; Schmitt et al. 2019, 2022; Cook et al. 2024; Tebbett et al. 2024). Fishing pressure on herbivorous fish is increasing globally, reducing their populations and impairing their ecological roles (Bellwood et al. 2004; Hughes et al. 2007; Bonaldo et al. 2014; Vergés et al. 2016; Robinson et al. 2020; Foo et al. 2021; Akita et al. 2022; Feitosa et al. 2023; Leitão et al. 2023; Asbury et al. 2024; Cook et al. 2024). Given their taxonomic and functional diversity, herbivorous fish target various benthic algae at different growth stages, further highlighting their importance in ecosystem functioning (Bellwood et al. 2004; Hughes et al. 2007; Plass-Johnson et al. 2015; Kelly et al. 2016; Mumby 2016; Siqueira et al. 2019; Pombo-Ayora et al. 2020; Sheppard et al. 2023).

Through top-down control, herbivorous fish regulate benthic structure and habitat complexity via algal consumption (Mumby et al. 2006; Bonaldo et al. 2014; Adam et al. 2015b; Bozec et al. 2016; Campbell et al. 2018; Ruttenberg et al. 2019). However, much of the research supporting this idea has focused on Caribbean reefs, and it is uncertain whether these mechanisms apply equally in other regions (Roff and Mumby 2012). In some cases, bottom-up processes, such as benthic habitat characteristics, may play a more significant role in determining fish populations (Friedlander and Parrish 1998; Friedlander et al. 2003; Messmer et al. 2011; Russ et al. 2021; Tony et al. 2021; Zuercher et al. 2023; Rempel et al. 2024). Studies conducted in the Philippines have highlighted strong bottom-up effects on parrotfish populations (Russ et al. 2015, 2018), with similar patterns observed in the Indian Ocean (Samoilys et al. 2018; Ricot et al. 2024). These system-specific differences suggest the need for more research to better understand the mechanisms at play in different coral reef ecosystems, as such patterns may vary across different parts of the Western Indian Ocean (WIO), depending on habitat type and the degree of fishing pressure.

Rodrigues Island hosts some of the most extensive coral reefs in the Indian Ocean (Bhagooli and Kaullysing 2019). The island's population has been engaged in fishing activities since the mid-18th century, with overfishing becoming an important issue by the early 20th century (Heemstra et al. 2004). Fishing methods, including seine nets, basket traps, and hook and line, have contributed to the decline of coral reef health, compounded by additional pressures from sedimentation, sea-level rise, cyclones, agricultural runoff, coral bleaching, coral diseases, and climate change (Heemstra et al. 2004; Turner and Klaus 2005; Klaus 2017; Bhagooli and Kaullysing 2019; Bhagooli et al. 2021; Jogee et al. 2023). This study aimed to explore the relationship between benthic characteristics and herbivorous fish populations around Rodrigues Island. Specifically, we examined herbivorous fish communities in two different habitat types: one with high live coral cover and low algal cover ("coral-dominated") and another with intermediate coral cover and intermediate or high algal cover ("non-coral-dominated"). We hypothesize that the composition of herbivorous fish assemblages and their foraging patterns will vary between these two habitat types.

MATERIALS AND METHODS

Site description

Rodrigues Island (19°42′59.99″ S, 63°24′59.99″ E) (Figure 1) is an outer autonomous island of the Republic of Mauritius that forms part of the Mascarene Islands. The island is situated in the southwestern part of the Indian Ocean (Figure 1.A) at around 560 km to the east of the island of Mauritius. The island measures 18 km in length and 6.5 km in width, with a total land area of 108 km^2. The island is surrounded by a large fringing reef, with an estimated area of 230.6 km^2 (Turner and Klaus 2005; Bhagooli and Kaullysing 2019). There are also four marine reserves (Passe Demie, Grand Bassin, Anse aux Anglais, and Rivière Banane) and one multiple-use marine protected area (South East Marine Protected Area - SEMPA) around the island (Figure 1.B). The chosen survey sites exhibited diverse levels of conservation measures and were subsequently categorized as either protected or non-protected based on their respective management protocols.

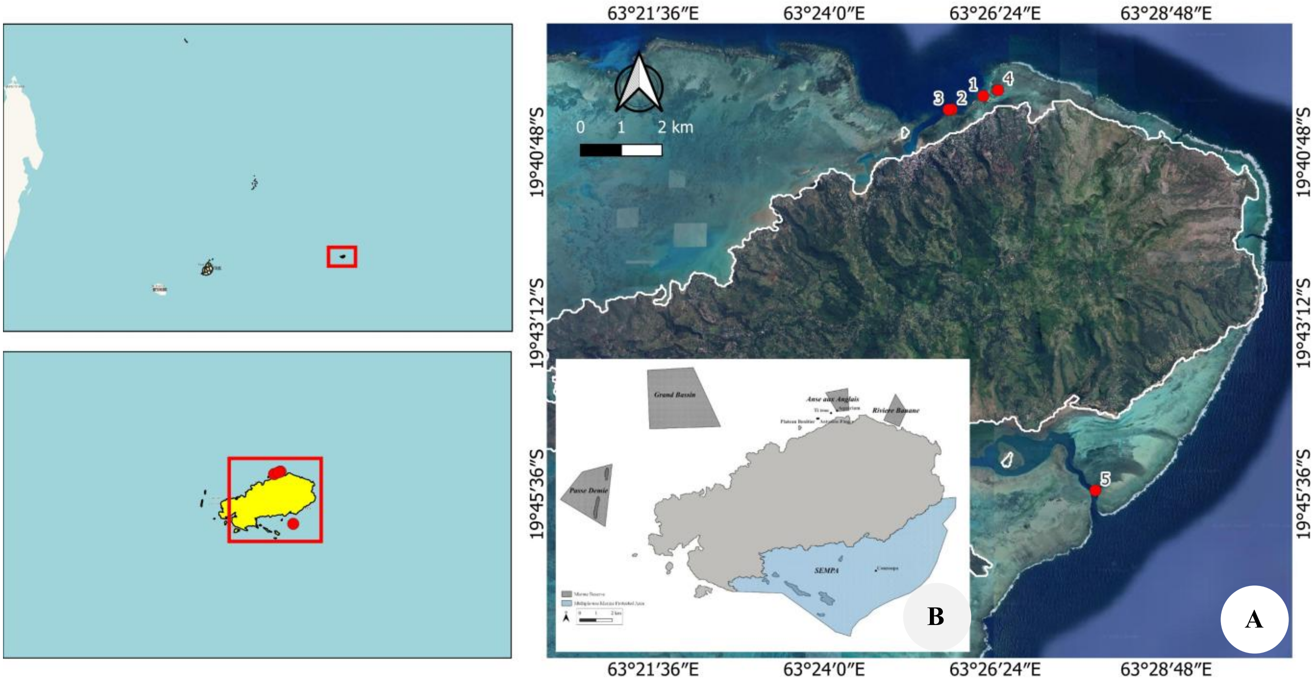

Figure 1. A. Location of Rodrigues Island in the Indian Ocean. B. Map of Rodrigues showing study sites around Rodrigues Island, Republic of Mauritius. 1. Ti Trou, 2. Antonio's Finger, 3. Plateau Bénitier, 4. Aquarium, 5. Couzoupa

Table 1. Summarized description of surveyed sites around Rodrigues Island

Sites	Depth (m)	Protected/non-protected	Coral-dominated/non-coral-dominated
Ti Trou	6-9	Non-protected	Coral-dominated
Antonio's Finger	6-9	Non-protected	Non-coral-dominated
Plateau Bénitier	6-9	Non-protected	Non-coral-dominated
Aquarium	6-9	Protected	Non-coral-dominated
Couzoupa	9-12	Protected	Coral-dominated

Table 2. Description of the different benthic categories

Benthic category	Definition
Live Hard Coral	Living stony corals with visible tissue and intact structure.
Dead Coral	Standing coral skeletons without living tissue.
Coral Rubble	Loose or broken pieces of dead coral lying on the seafloor.
Algae	Includes turf algae and macroalgae growing on the reef surface.
Sand	Unconsolidated, soft substrate made of fine particles or sediment.
Red coralline algae	Hard, encrusting or branching algae with a pink to deep red, often rough and calcareous surface that forms crusts or plates on rocks and coral reefs

This study was conducted from 17 to 20 December 2020. Five study sites (Table 1), namely Aquarium, Plateau Bénitier, Ti Trou, Antonio's Finger, and Couzoupa, were chosen around the island. Sites were selected based on logistical accessibility and prevailing daily weather conditions. Couzoupa is situated in the SEMPA and Aquarium in the Anse aux Anglais Marine Reserve. At the same time, all the other sites are located in a non-protected area in the northeast of Rodrigues. The classification of sites as coral-dominated or non-coral-dominated was based on the criteria established by McField and Kramer (2007), which define high live coral cover as hard coral accounting for more than 20% of the total benthic cover. Accordingly, sites with live coral cover exceeding 20% were classified as coral-dominated, while those with less than 20% were categorized as non-coral-dominated. The classification of sites as coral-dominated or non-coral-dominated was determined after data collection, based on the measured percentage of live hard coral cover recorded during the benthic surveys.

Benthic survey

The benthic cover was assessed in situ using visual estimation by a diver conducting surveys along a 50 m line-intercept transect. Surveys were conducted across sites with depths ranging from 6 m to 12 m. At each site, three 50 m transects were deployed, maintaining a minimum spacing of 15 m between transects. The percentage cover of live hard coral, dead coral, coral rubble, algae, red coralline algae and sand (each benthic category recorded is detailed in Table 2) was recorded following the methodology outlined by English et al. (1997). The number of transects per site was limited to three due to time constraints.

Fish surveys

Surveys were performed using scuba diving along 50×2 m belt transects, with three replicate transects deployed per site. Hence, to minimize potential biases associated with diver presence, such as fish displacement (push-pull effects), transects were spaced at least 15 m apart.

All individuals from the families Acanthuridae and Scaridae with a total length ≥3 cm were recorded and identified to species level. The Acanthuridae and Scaridae families were selected, as they represent two of the most frequently encountered reef fish families within the herbivorous trophic group. To ensure methodological consistency and minimize observer-related variability, a single observer conducted all surveys. Herbivorous fish were classified following criteria established by Ferreira et al. (2004) and Samoilys et al. (2018).

Fish biomass was estimated using species-specific length-weight relationships (Letourneur 1998). All recorded individuals from the Acanthuridae and Scaridae families with a total length (TL)≥3 cm were categorized into five size classes: 3-10 cm, 11-20 cm, 21-30 cm, 31-40 cm, and >40 cm. A representative length was assigned to each size category to facilitate biomass calculation. Individual weights were derived using the appropriate length-weight coefficients for each species. Estimated weights were calculated for each individual and subsequently aggregated at the transect level. Biomass was expressed in kilograms per hectare (kg/ha).

Data analysis

The data were organized into a series of matrices: benthic cover variable percentage, biomass of Acanthuridae, biomass of Scaridae. The Shapiro-Wilk test was used to assess the normality of the data. Natural $\log_{10}$ transformation was conducted on non-normal data ($p<0.01$) prior to conducting additional statistical analysis. The raw data failed to pass normality tests. Then, to determine any significant differences in biomass of Acanthuridae and Scaridae and benthic variable percentage among the surveyed sites around Rodrigues, the non-parametric Kruskal-Wallis test was utilized. The Mann-Whitney U Test (with Bonferroni correction) was used to test for any significant differences ($\alpha=0.05$) in the benthic variable percentage and the biomass of Acanthuridae and Scaridae between the coral-dominated and non-coral-dominated sites. A two-way ANOVA was used to test for the effects of protection status, live coral cover, and their interaction on the biomass of Acanthuridae and Scaridae. Fish assemblage structure was characterized using the Shannon-Wiener diversity index (H′) and Pielou's evenness index (J′). All statistical analyses were conducted using MS Excel, SPSS (IBM Version 27), and XLSTATS Version 2023.3.0 (Lumivero 2024). Next, to investigate the associations between Acanthuridae and Scaridae fish families and benthic variables across survey sites, a Canonical Correspondence Analysis (CCA) was generated using XLSTAT Version

2023.3.0 (Lumivero 2024). The CCA was chosen for its suitability in examining the relationships between multivariate ecological data and environmental gradients, particularly when working with count or proportion data.

RESULTS AND DISCUSSION

Benthic composition

The benthic cover varied among the different surveyed sites around Rodrigues Island. A significant difference was observed in live coral cover (p=0.04), dead coral (p=0.037), algae (p=0.02), and red coralline algae (p=0.039) and across the sites (p<0.05), with live coral cover ranging from 64.03±9.55% to 7.3±1.32% (Figure 2). Couzoupa displayed the highest live coral cover, while Plateau Bénitier had the lowest live coral cover, nearly 9-fold lower than at Couzoupa. Dead coral cover ranged from 1.93±1.33% to 33±20.56%. The highest dead coral cover was recorded at the Aquarium, while the lowest was at Couzoupa**.** Rubble cover varied across sites, with Ti Trou exhibiting the highest rubble cover (40.6±13.16%), while Plateau Bénitier had the lowest rubble cover (16.8±1.78 %). Algal cover was highest at Plateau Bénitier (61.47±8.76 %), and red coralline algae was highest at Antonio's Finger, which had 23.53±17.71% cover. A significant difference was observed in live coral cover, algae, and red coralline algae between the coral-dominated and non-coral-dominated habitats.

The biomass of the Acanthuridae and Scaridae families, expressed in kg/ha, exhibited notable variation across the study sites; however, statistical analysis indicated significant differences in biomass of the Acanthuridae family only among the sites (p=0.03). Couzoupa recorded the highest biomass for both families, with Acanthuridae at 1,040.15±348.33 kg/ha and Scaridae at 798.96±304.15 kg/ha (Figure 3). Antonio's Finger also displayed relatively high biomass values, with Acanthuridae at 795.44±104.74 kg/ha and Scaridae at 289.21±115.10 kg/ha. In contrast, Plateau Bénitier exhibited the lowest biomass for both families, with Acanthuridae at 346.65±87.15 kg/ha and Scaridae at 139.61±121.51 kg/ha.

A total of 13 herbivorous fish species were identified across two habitats. Seven of these belong to the family Acanthuridae (surgeonfishes) and six to the family Scaridae (parrotfishes) (Figure 4). Of all the species, 12 were recorded in the non-coral-dominated (Figure 4.A) habitat and 10 in the coral-dominated (Figure 4B). The highest biomass was recorded for the species *Acanthurus mata* for the non-coral dominated habitats (358.23±194.13 kg/ha). In contrast, for the coral-dominated habitat, the *Chlororus sordidus* exhibited the highest biomass (388.09±361.34 kg/ha). The total biomass was higher in the coral-dominated habitats compared to non-coral-dominated habitats. However, the total biomass of individuals (kg/ha) showed no significant difference in the coral-dominated (1,028.54±847.78 kg/ha) and the non-coral-dominated (728.34±229.36 kg/ha) habitats. Moreover, no significant differences (p>0.05) were observed in the biomass of Acanthuridae and Scaridae between coral-dominated (641.7±494.3 kg/ha and 486.90±399.2 kg/ha, respectively) and non-coral-dominated habitats (538±218 kg/ha and 190.30±148.10 kg/ha, respectively). Shannon-Wiener diversity index was higher in coral-dominated habitats, with a value of 1.47, compared to 1.38 in non-coral-dominated habitats. Evenness was also greater in coral-dominated areas, reaching 0.64, while non-coral-dominated areas had a lower evenness of 0.56.

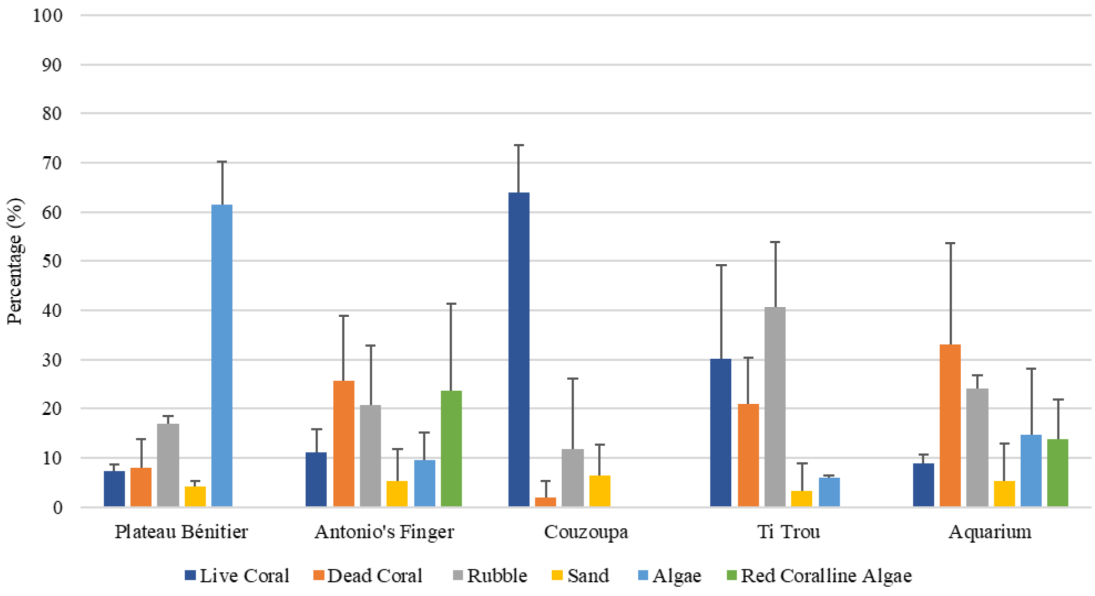

Figure 2. Benthic cover at the five surveyed sites around Rodrigues Island (bars represent mean ± standard deviation)

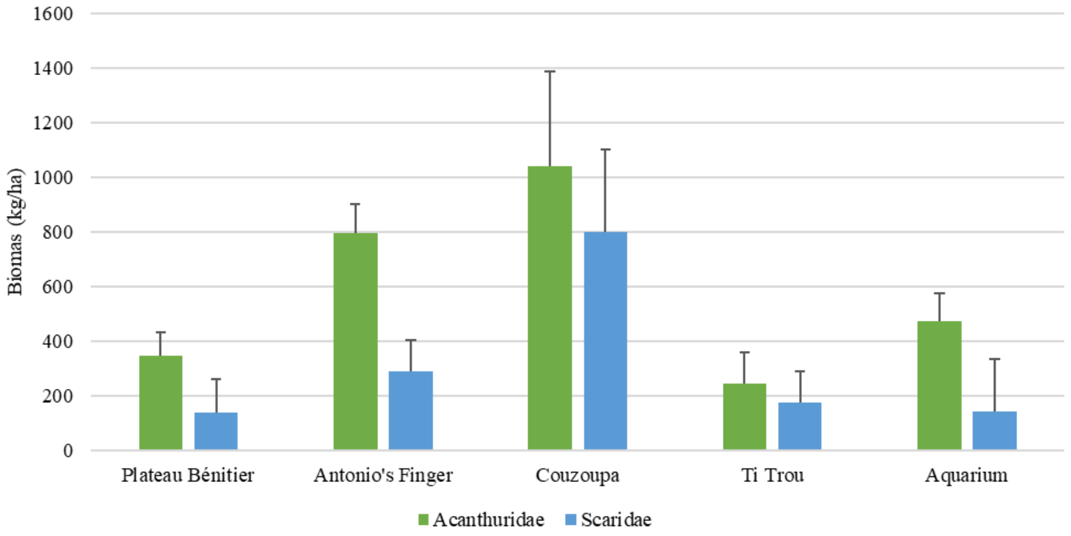

Figure 3. Biomass of the Acanthuridae and Scaridae at five studied sites around Rodrigues (bars represent mean ± standard deviation)

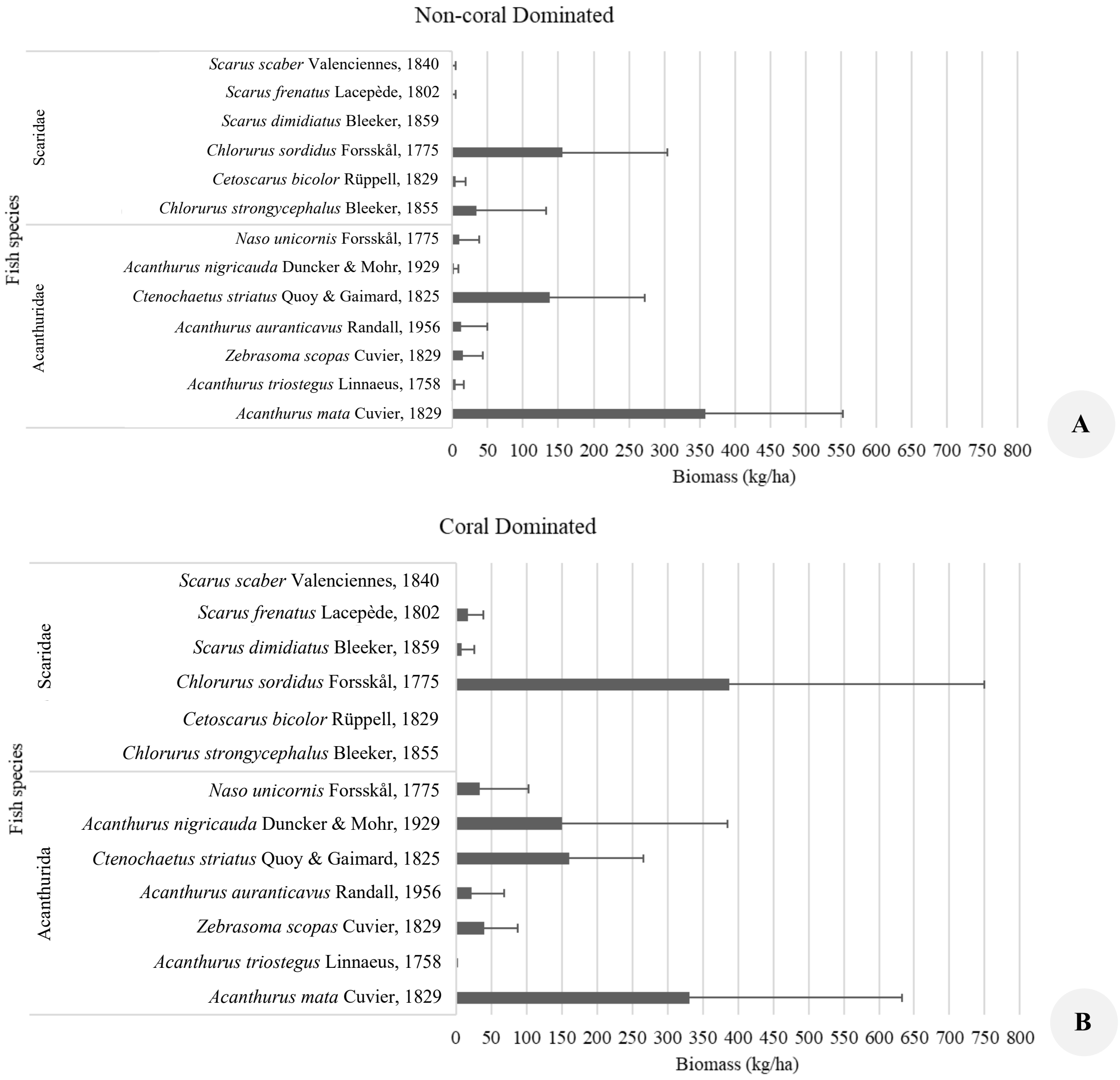

Figure 4. Biomass (kg/ha) of herbivorous fish species surveyed in A. The non-coral-dominated habitats, B. The coral-dominated habitats (bars represent mean ± standard deviation)

The effects of protection, live coral, and their interaction on the biomass of Acanthuridae and Scaridae revealed no significant main effects for protection or live coral on the biomass of either family (Table 3). Specifically, protection did not significantly influence the biomass of Acanthuridae (F=3.918, *p*=0.105) or Scaridae (F=4.289, *p*=0.093), nor did live coral cover have a significant effect on Acanthuridae (F=0.636, *p*=0.461) or Scaridae (F=0.525, *p*=0.501). However, a significant interaction effect was observed for Acanthuridae (F=11.074, *p*=0.021) and Scaridae (F=6.193, *p*=0.045), indicating that the combined influence of protection status and live coral cover levels significantly affected the biomass of these fish families.

The CCA biplot (Figure 5) illustrates the relationships between benthic habitat types and reef fish communities, with the first two principal components explaining 79.10% of the total variance (F1: 53.31%, F2: 25.79%). The active variables (red vectors) represent benthic habitat types and reef fish families, while the active observations (blue points) indicate sampling sites.

Live coral and sand are positively correlated with F1, alongside fish families such as Scaridae and Acanthuridae, while rubble, red coralline algae, and dead coral are associated with F2. Sampling sites such as Couzoupa are strongly aligned with live coral and Scaridae, whereas sites like Aquarium and Antonio's Finger are associated with dead coral, red coralline algae, and rubble. Ti Trou and Plateau Bénitier exhibit alignment with rubble and algae.

Table 3. Effects of protection, live coral cover, and their interaction on the biomass of Acanthuridae and Scaridae

Source	Dependent variable	F	Sig.
Protection	Acanthuridae	3.918	0.105
	Scaridae	4.289	0.093
Live coral cover	Acanthuridae	0.636	0.461
	Scaridae	0.525	0.501
Protection * Live coral cover	Acanthuridae	11.074	0.021
	Scaridae	6.193	0.045

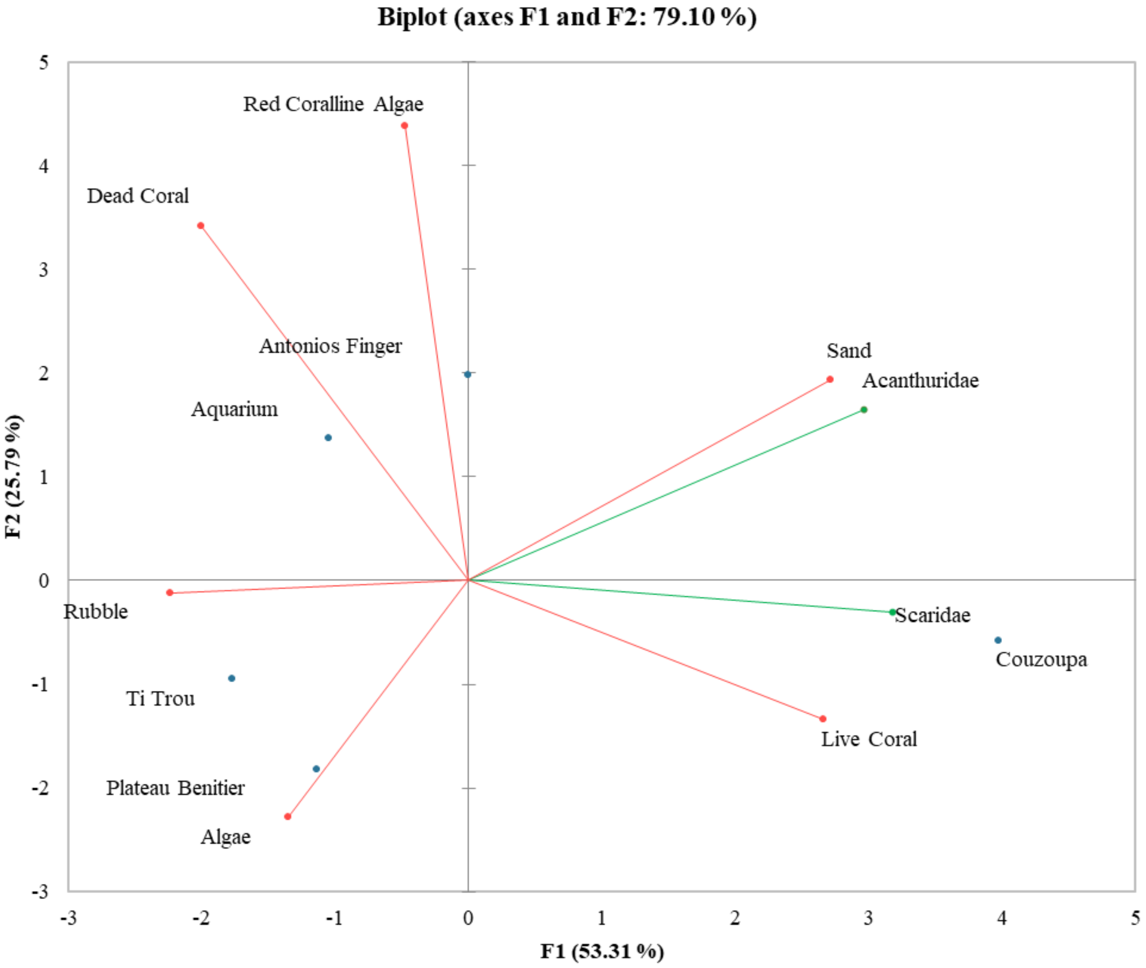

Figure 5. CCA biplot showing the relationships between benthic habitat types (red), reef fish families - Acanthuridae and Scaridae (green), and sampling sites (blue)

Discussion

In coral-dominated habitats, the highest biomass, diversity, and evenness of herbivorous fish were recorded. This suggests that coral-dominated habitats (sites with more than 20% live coral cover), could thus be providing essential habitat and dietary resources for an assemblage of herbivorous fish with higher species diversity. The positive association between live coral cover, benthic complexity, and fish community structure has been widely documented, with previous studies highlighting the role of structurally complex reef environments in sustaining high fish abundance and biomass (Jones et al. 2004; Messmer et al. 2011; Pratchett et al. 2011; Chong-Seng et al. 2012; Graham et al. 2015; Holbrook et al. 2015; Darling et al. 2017; Richardson et al. 2017, 2020; Russ et al. 2021; Helder et al. 2022; Fisher 2023).

The higher evenness observed in coral-dominated habitats indicates a more balanced distribution of ecological traits among herbivorous species compared to non-coral-dominated areas. In contrast, herbivorous fish in non-coral-dominated habitats exhibited lower biomass, species diversity, and evenness. Notably, parrotfish (Scaridae) species, which play a crucial role in removing turf algae and sediments (Adam et al. 2018; Abu-Taweel et al. 2023; Randazzo-Eisemann et al. 2024), had the lowest biomass in the non-coral dominated habitats. Similarly, apart from *A. mata,* most of the surgeonfish species that contribute to sediment removal, turf clearance, and crevice cleaning were less abundant, resulting in a functional decline within the herbivorous assemblage. The reduced structural complexity and limited live coral cover in non-coral-dominated habitats likely constrain niche availability and diminish protection from predators. Shelter from predators is an important resource in coral reef environments (Catano et al. 2016; Kerry and Bellwood 2016) and ultimately shapes the observed differences in herbivorous fish assemblages. While the ecological roles of herbivorous fish can differ depending on the habitat preference, the total biomass of herbivorous fish which presented no significant difference between coral-dominated and non-coral-dominated habitats remained an essential ecological component across all habitats, with their role in maintaining ecosystem balance being ecologically significant even in non-coral systems (Hardman et al. 2010). This is further reinforced by the knowledge that, even in severely damaged coral reef systems, fish herbivory is an essential ecological function (Plass-Johnson et al. 2015).

Habitat characteristics that benefit herbivorous fish in one environment may not have the same influence in another, as different environmental factors drive variations in fish abundance and biomass across habitat types. The close association observed between live coral cover and the Scaridae family may be attributed to the structural complexity associated with this benthic category (Friedlander and Parrish 1998). This aligns with broader trends indicating that higher biomass of larger reef fish, including Scaridae, is often correlated with structurally complex coral colonies (Roos et al. 2019; Fisher 2023; Sheppard et al. 2023). In contrast, Acanthuridae were more strongly associated with the benthic variable sand, consistent with findings from Hoey and Bellwood (2011) from the Great Barrier Reef, where herbivorous fish demonstrated a preference for open substrates over dense macroalgal stands. Herbivore habitat selection may also be influenced by top-down processes, particularly if refuge availability or the capacity to detect and evade predators is linked to habitat structure (Hoey and Bellwood 2011). In marine ecosystems, structural complexity is widely recognized as a key factor in mitigating predation pressure (Hensel et al. 2019; Santano et al. 2021; Chang and Todd 2023). Increased habitat complexity, provided by corals in tropical environments, has been shown to reduce fish mortality by offering spatial refuge from predators (Anderson 2001; Holbrook and Schmitt 2002). The apparent avoidance of structurally complex patches by certain herbivorous fish species may reflect an aversion to habitats where predator presence is likely rather than a direct response to predation itself (Verdolin 2006). Additionally, coral-dominated habitats by exhibiting increased structural complexity, also support a greater diversity of foraging niches, which collectively contribute to sustaining higher biomass levels of herbivorous fish, particularly within grazing guilds (Brooker et al. 2013; Wen et al. 2013). In contrast, habitats with low coral cover generally possess lower structural heterogeneity, thereby reducing both the availability of shelter and the quality of feeding substrates, ultimately limiting their capacity to support dense herbivorous fish populations (Sánchez-Caballero et al. 2016; Ho et al. 2018).

Marine Protected Areas (MPAs) serve as an essential management tool for conserving marine resources and habitats by restricting activities that contribute to habitat degradation (Cortés-Useche et al. 2021). Our findings indicate that the coral-dominated site Couzoupa, located within an MPA and exhibiting the highest live coral cover among the studied sites, together with the significant interaction effect observed for herbivorous fish families Acanthuridae and Scaridae suggests that both protection status and coral cover levels play a key role in shaping their biomass. These results align with previous studies demonstrating that effective MPA management enhances reef fish communities, leading to increased fish density and biomass (Halpern and Warner 2002; Muallil et al. 2015; Chirico et al. 2017; Cabral et al. 2020; McClure et al. 2020; Thiaw et al. 2021; Ziegler et al. 2022; Frid et al. 2023).

The ecological significance of coral reefs within MPAs further underscores the need for targeted conservation measures. In Rodrigues, corals are considered the most well-developed and substantial in the Mascarene region (Montaggioni and Faure 1980; Bhagooli and Kaullysing 2019) and play a crucial role in ecosystem functioning, including carbon cycling (Fenner et al. 2004; Payet and Agricole 2006). The association of the coral-dominated site Couzoupa with live coral cover, shown by the results and the significant interaction effect for the herbivorous fish Acanthuridae and Scaridae, highlights the importance of protecting these foundational habitats to sustain reef fish populations. Given the small size of Rodrigues Island and the pressures on its coastal resources (Heemstra et al. 2004; Turner and Klaus 2005; Klaus 2017; Bhagooli and Kaullysing 2019; Bhagooli et al. 2021), MPAs provide a valuable framework for safeguarding reef ecosystems while supporting sustainable fisheries management as part of an integrated coastal zone management strategy (Bunce et al. 2008; Costello and Ballantine 2015; Cortés-Useche et al. 2021; Grorud-Colvert et al. 2021; Horta e Costa et al. 2022; Masud et al. 2022; Nowakowski et al. 2023). These findings emphasize the critical role of habitat structure in shaping herbivorous fish assemblages and highlight the need for continued monitoring and adaptive management strategies to ensure the long-term sustainability of coral reef ecosystems on Rodrigues Island.

In conclusion, the results of this study highlight the critical role of live coral cover in sustaining herbivorous fish biomass around Rodrigues Island. While no significant differences were observed in the biomass of the Acanthuridae and Scaridae fish families between coral-dominated and non-coral-dominated sites, the significant interaction between protection status and live coral cover indicates that the combination of effective management and habitat restoration may play a crucial role in supporting herbivorous fish populations. Future research should focus on investigating temporal variations in herbivorous fish biomass and benthic composition to understand the long-term stability of these communities better. Furthermore, incorporating additional environmental variables such as ocean currents, temperature, and nutrient availability would provide a more refined understanding of the factors driving the observed ecological patterns. The limitations of this study, including the relatively small number of transects and the spatial scale, should be acknowledged. Larger-scale, long-term studies are necessary to obtain more robust and generalizable data, enabling a more comprehensive understanding of the complex interactions between benthic habitats, fish populations, seasonal variability, and conservation management. Such research will be essential for informing more effective, evidence-based conservation strategies aimed at preserving the integrity and function of coral reef ecosystems.

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Spatio-temporal density patterns of corallivorous invertebrates around Rodrigues Island, Western Indian Ocean

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Abstract. *Priest JS, Ramah S, Ramkalam M, Korimbocus AM, Bhagooli R, Kaullysing D. 2025. Spatio-temporal density patterns of corallivorous invertebrates around Rodrigues Island, Western Indian Ocean. Indo Pac J Ocean Life 9: 92-99.* Coral reef ecosystems globally are subject to multiple stressors making them targets for corallivore predation by organisms such as the crown-of-thorns starfish (COTS), *Acanthaster* (Gervais 1841) and gastropods, mainly *Drupella* (Thiele 1925). Around Rodrigues Island, little is known about COTS and gastropod corallivory. Surveys to assess COTS and *Drupella cornus* (Röding 1798) density were conducted using the belt transect method and random quadrat sampling, respectively, around Rodrigues Island from 2017 to 2020 at least once at six lagoon sites (1-2 m). In April 2024, additional surveys were carried out at nine lagoon sites (1-2 m) and seven dive sites (9-28 m), including previously surveyed locations. During this study, no COTS were observed along the surveyed transects, however, suspected COTS feeding scars were spotted on some coral colonies at two lagoonal sites. Significant spatio-temporal variations in *D. cornus* density were observed, with considerable increases at Rivière Banane from 0.07 ± 0.07 ind/m^2 in 2018 to 0.93 ± 0.48 ind/m^2 in 2024 and Var Brûlée from 0.40 ± 0.16 ind/m^2 in 2017 to 2.07 ± 0.89 ind/m^2 in 2024. Two-way ANOVA test revealed significant interaction between site and year ($p < 0.01$), suggesting that both spatial (site) and temporal (year) factors interact in influencing *D. cornus* densities. These findings suggest potential reef stress, possibly caused by fishing pressure, predator loss, and/or rising sea temperatures, and highlight the necessity for corallivore monitoring and intervention to protect the health and resilience of the coral reefs of Rodrigues. The study revealed that *D. cornus*, rather than COTS, poses a potential threat to Rodrigues reefs, particularly at Var Brûlée and Rivière Banane. Further research is warranted to gather additional data on corallivore distribution and their impact on the coral reefs of Rodrigues.

Keywords: *Acanthaster*, corallivory, crown-of-thorns starfish, *Drupella cornus*, Rodrigues

Abbreviations: COTS: Crown-of-thorns starfish, WIO: Western Indian Ocean

INTRODUCTION

Corals are diverse and important organisms, particularly scleractinian corals as they are reef- or habitat-building corals essential for coral ecosystem productivity, promoting nutrient recycling, primary production, and reef development (Pratchett et al. 2008). However, these vital ecosystems are under multiple anthropogenic and natural, regional and local-scale threats such as deleterious fishing practices and overfishing, coral diseases, climate change, and poor water quality stemming from land-based pollution, all of which are exerting extreme pressure on these fragile ecosystems and influencing their functioning, making them susceptible to corallivore predation (Souter et al. 2021). Corallivores such as the crown-of-thorns starfish (*Acanthaster* Gervais, 1841 - COTS) and gastropods such as *Drupella* (Thiele, 1925) and *Coralliophila* (H. Adams & A. Adams, 1853) are contributors to global coral reef degradation by predating on stressed corals (Tsang and Ang 2015; Kaullysing et al. 2016; Zhang et al. 2024). The indicative sign of corallivores feeding on corals in an area is the white scar left behind on the coral, symptomatic of the loss of living coral tissue (Kaullysing et al. 2017; Gautrand et al. 2023). Corallivore outbreaks of species such as *Acanthaster* spp. and *Drupella* spp. have been reported on coral reefs globally.

COTS predate primarily on scleractinian corals such as *Acropora* spp. (Oken 1815) but can diversify their diets to soft corals and molluscs when coral prey is limited (Pratchett et al. 2017). COTS can cause massive depletion of living hard coral cover of up to 90% as they can consume up to 150 to 250 cm^2 of live coral tissue daily (Souter et al. 2021). COTS outbreaks have been reported globally throughout the Indo-Pacific Ocean. The Island of Moorea had more than 96% of its corals killed due to high COTS densities from 2005 to 2010 (Kayal et al. 2012), and COTS have contributed to 50% reduction in live hard coral from 1985 until 2012 in the Great Barrier Reef (Westcott et al. 2020). Specifically, in the Southern Indian Ocean, COTS outbreaks were recorded in South Africa's Two-mile Reef during the 1990s, lasting almost 10 years and peaking between

1994 and 1996 (Celliers and Schleyer 2006). Outbreaks were also reported in the Seychelles in 1997 and 2014, and in Mauritius at certain sites in 2014 (Obura et al. 2017; Uthicke et al. 2023). Although published scientific data on COTS distribution around the Republic of Mauritius is currently scarce, Ramah et al. (2021) reported observing a single *Acanthaster* sp. individual at Saya de Malha Bank. There are five known COTS species, and they are relatively geographically defined throughout the Indian and Pacific Oceans. The COTS commonly found in the Southwest Indian Ocean is *Acanthaster mauritiensis* de Loriol, 1885 species (Uthicke et al. 2023).

The less conspicuous corallivorous *Drupella* spp., distributed in the shallow waters of the tropical and sub-tropical Indo-Pacific region, feed predominantly on branching *Acropora* spp., which comprises up to 80% of their diet (Raymundo et al. 2016; Bessey et al. 2018). Outbreak densities of *Drupella* spp. range from 1.4 to 6.4 ind/m^2 (Cumming 2009). *Drupella* spp. outbreaks have been recorded throughout the Pacific and Indian Oceans, whereby four massive population outbreaks of *Drupella* in the South Pacific Ocean were recorded in 1983, 1989, 1993, and 2014 to 2016 (Zhang et al. 2024). While several scientific studies on corallivory by gastropods (Kaullysing et al. 2016, 2017, 2019, 2020) and fish (Tiddy et al. 2021, 2023; Ricot et al. 2023) are available for Mauritius, the presence and impact of corallivores on the coral reefs of Rodrigues Island is largely unknown as the published information on corallivores in Rodrigues is limited. Rodrigues is considered a biological hotspot, and despite the ecological importance of the reefs of Rodrigues, very few studies on coral predation have been conducted, presenting a crucial data gap concerning corallivory in Rodrigues. Thus, this study aimed at observing the presence of corallivores and assessing the density of corallivorous invertebrates (*Acanthaster* spp. and *Drupella cornus*) on coral reefs around Rodrigues Island to understand corallivore dynamics and to provide essential baseline data needed for reef conservation efforts.

MATERIALS AND METHODS

Study area

Rodrigues, a remote island in the Western Indian Ocean, is situated about 560 km east of Mauritius (Figure 1). Rodrigues is located at the eastern end of an east-west trending ridge that intersects the Mascarene Plateau, and it does not share the same geological origin as the other Mascarene Islands. As an autonomous outer island of the Republic of Mauritius, Rodrigues spans roughly 108 km^2 with a hilly terrain, beaches and coral reefs. It has a vast lagoon area covering 300 km^2 bordered by a 200 km^2 fringing reef. The island's relatively unchartered marine waters appear to host a rich biodiversity (Bhagooli and Kaullysing 2019).

Field surveys

Surveys were carried out by snorkelling around Rodrigues Island at lagoon sites (1-2 m), namely, Rivière Banane, Pointe Coton, St François, Passe Semone, Var Brûlée, and Couzoupa_S (shallow waters) at least once in April from 2017 to 2020 to assess crown-of-thorns starfish (COTS) and corallivorous gastropods density. Additionally, in April 2024, snorkelling or SCUBA diving surveys were conducted once at each of 16 lagoonal (shallow) and dive sites around Rodrigues (Figure 1) to assess the distribution and density of the corallivores, including the sites surveyed at least once during the period 2017-2020. The lagoon sites (1-2 m) surveyed in 2024 were Rivière Banane, Pointe Coton, Anse Ali, St François, Passe Semone, Var Brûlée, Hermitage Island, Paté Reynieux, and Couzoupa_S, and the dive sites (9-28 m) were Antonio's Finger, Aquarium, Plateau Bénitier, Ti Trou, Couzoupa_D, Tombant Coco, and Ti Pate. It is noteworthy that restricted temporal coverage and potential under-detection of cryptic or nocturnal individuals may lead to underestimation of true population densities and spatial coverage. Site selection was largely determined by accessibility and historical coral cover.

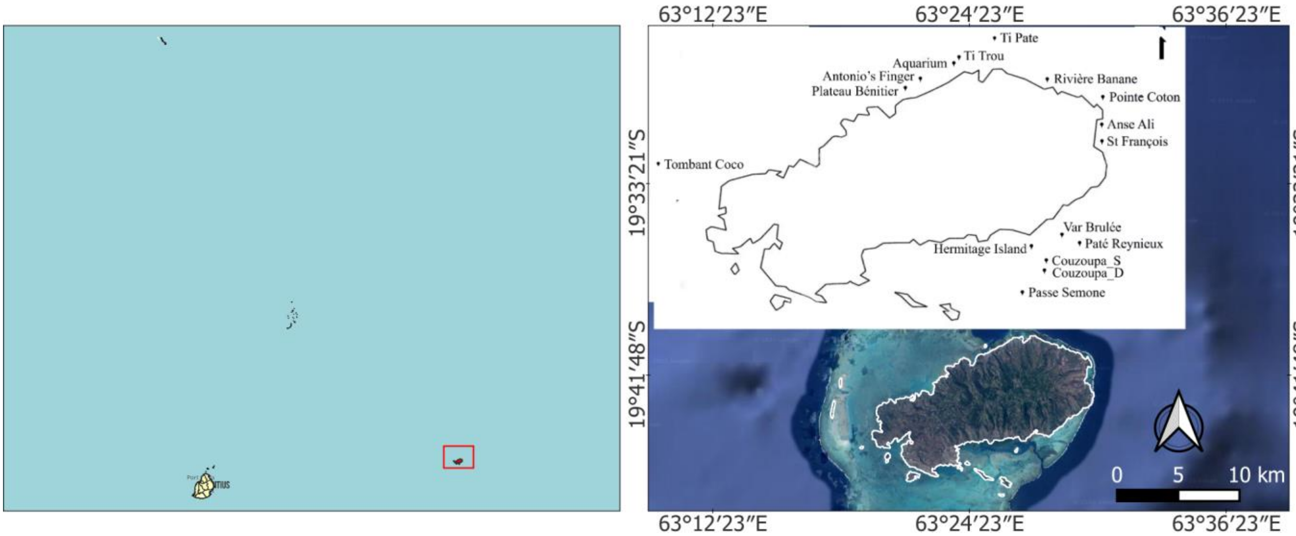

Figure 1. Study sites around Rodrigues Island, Mauritius

At each survey site, the belt transect method was used to assess COTS density (Samanthi 2021). Three belt transects each of 30 × 10 m (300 m^2), at 10 m intervals, were randomly laid to conduct a thorough search for COTS by direct observation, totalling a survey area of 900 m^2 at each site. The same belt transects were then used to conduct the line-intercept transect method to determine hard coral cover at each site. For corallivorous gastropod surveys, random quadrat method was used wherein 15 quadrats of 1 m^2 each were laid on coral colonies. *Drupella cornus* individuals were identified *in-situ* based on their shell morphology - distinct elongated conical shells with prominent axial ribs (Kaullysing et al. 2016), following morphological descriptions provided in standard identification guides for Indo-Pacific gastropods.

Invertebrate corallivore density measurements

The density of invertebrate corallivores was determined by counting the number of individuals present on the corals within each quadrat/belt transect and was expressed as the mean number of individuals/m^2 (ind/m^2). The species of coral upon which the invertebrates was also noted. The corallivores and the feeding scars were photographed using a digital camera (Olympus Tough TG-6 and TG-7).

Data analysis

Spatial maps were produced using QGIS software and all statistical analyses were performed in IBM SPSS Statistics 21. The Shapiro-Wilk test was used to assess the normality of the data. Arcsin(sqrt) transformation was applied to non-normal data before conducting further statistical analysis. A two-way ANOVA test ($\alpha = 0.05$) was performed to determine significant difference in the mean number of *D. cornus* across all sites and years of study. The two-way ANOVA test was performed on sites with repeated surveys, sites surveyed only once were excluded from the analysis.

RESULTS AND DISCUSSION

Crown-of-thorns starfish assessment

COTS were not observed during the surveys along the belt transects in any year at the study sites. The lack of sightings of COTS was uniform across all sites with varying depths, coral species and structural complexity, suggesting that such an observation was not restricted to a particular habitat type. Generally, outbreaks of COTS have been linked to significant coral degradation in various regions (Deaker and Byrne 2022; Foo et al. 2024). The lack of observed COTS in the present study along the surveyed transects suggests that local environmental conditions, effective natural predation, or recent management interventions might be inhibiting the proliferation of this coral predator. This tends to indicate a potentially stable status in terms of COTS predation for Rodrigues reef ecosystems. However, the lack of observation of COTS does not necessarily indicate their complete absence from the entire reefs around Rodrigues. It may also suggest that they possibly occur at very low densities. COTS in low densities are beneficial to coral reef ecosystems as they consume the faster-growing corals, such as *Acropora* spp., thus allowing the slower-growing coral species to proliferate, which improves the coral species diversity and richness of that coral reef and promotes greater biological diversity and ecological functioning (Foo et al. 2024).

Although no COTS were observed during the surveys, suspected feeding activity by COTS as large and distinct white patches was noted on some coral colonies at Rivière Banane (Figure 2.A) and Var Brûlée in April 2024 (Figure 2.B). COTS feeding scars were observed as white patches of recently dead coral, and were distinguished by their large, distinct, and striking white color (Figures 2.A and 2.B). While such scarring can be attributed to COTS feeding, it may also result from White Syndrome (Roff et al. 2011) or coral bleaching. In contrast, scars left by *Drupella* spp. tend to be less distinct (Figure 2.C), often exhibiting blurred edges due to the subsequent colonization of turf algae, except in the most recent feeding areas (Miller et al. 2018). The scars are generally more focused at the base of the coral.

Figure 2. Suspected COTS feeding scar on *Acropora* (Oken 1815) at A. Rivière Banane and B. Var Brûlée in 2024 in Rodrigues, C. *Drupella* (Thiele, 1925) feeding scars indicated by yellow arrows at St François in 2024

In Rodrigues, there are four no-take Marine Reserves located in the north of the island (Rivière Banane, Anse Aux Anglais, Grand Bassin, and Passe Demie), and a large Marine Protected Area, the South East Marine Protected Area (SEMPA), located in the Southeast region of the Island (Pasnin et al. 2016). The presence of these Marine Protected Areas (MPAs) could have contributed to the possible absence or low COTS densities as fisheries management has been seen to influence COTS densities. MPAs, including no-take reserves, can protect the predators of COTS, such as the giant *Triton* (Montfort 1810), triggerfish, and butterflyfish. A study by Kroon et al. (2021) indicated that no-take reserves affect COTS densities as these areas have high COTS predator densities which in turn regulates COTS densities and reduces their outbreak frequency. There could be a multitude of factors influencing the density of COTS around Rodrigues, such as the ‘predator removal hypothesis’ and the ‘terrestrial runoff hypothesis’ (Kroon et al. 2021), therefore, more research needs to be done to determine the factors regulating the densities of COTS around Rodrigues.

Drupella cornus (Röding, 1798) density

Even though no COTS individuals were found at the surveyed sites, another less-noticeable coral predator, *D. cornus*, was observed impacting six shallow reef sites, namely, Rivière Banane, Pointe Coton, St François, Passe Semone, Var Brûlée, and Couzoupa_S. In the Indo-Pacific, the exceptionally high densities of these snails seem to have caused widespread and severe coral mortality, a level of impact previously attributed only to the crown-of-thorns starfish, *Acanthaster planci* (Linnaeus, 1758) (Turner 1994). Considerable spatio-temporal variations in the mean density of *D. cornus* were revealed (Figure 3). *Drupella cornus* has remarkable camouflage ability. Its shell, which is often covered with red coralline algae, allows it to blend with the substrate, particularly under coral colonies, in between coral rubbles, and under algal-covered surfaces. This enables *D. cornus*, as well as other *Drupella* species, to escape predation during feeding activities.

In the present study, *D. cornus* was exclusively observed at shallow depths, with no individuals found in deeper reef zones at the dive sites. This pattern aligns with previous observations, that is, *Drupella* spp. show a strong habitat preference for sheltered reef slopes (Zhang et al. 2024). The tendency for aggregation at shallower depths (Dehnert et al. 2022) may be influenced by factors such as the availability of preferred coral hosts such as *Acropora* (Oken 1815), increased coral damage from wave action, or higher temperatures that may facilitate feeding and reproduction. The absence of *Drupella* at relatively greater depths could also reflect habitat specificity or predator pressures that vary with depth (Osuka et al. 2022).

One of the main observations from this study was the increase in *D. cornus* density at certain sites. At Rivière Banane, the density increased from 0.07 ± 0.07 ind/m^2 in 2018 to 0.93 ± 0.48 ind/m^2 in 2024, a more than 13-fold increase. Similarly, at Var Brûlée, *D. cornus* densities increased from 0.40 ± 0.16 ind/m^2 in 2017 to 2.07 ± 0.89 ind/m^2 in 2024 (> 5-fold increase), despite a temporary decrease in 2019 (Figure 3). This marked rise may reflect outbreak dynamics similar to those observed at Ningaloo Marine Park (Ayling and Ayling 1987), where *Drupella* feeding on *Acropora* spp. contributed to over 30% coral loss within two years. Notably, *D. cornus* was absent from surveyed quadrats at Passe Semone in 2018, but by 2024, densities reached 0.33 ± 0.27 ind/m^2, indicating that previously uninhabited or sparsely populated areas are now experiencing *D. cornus* population growth.

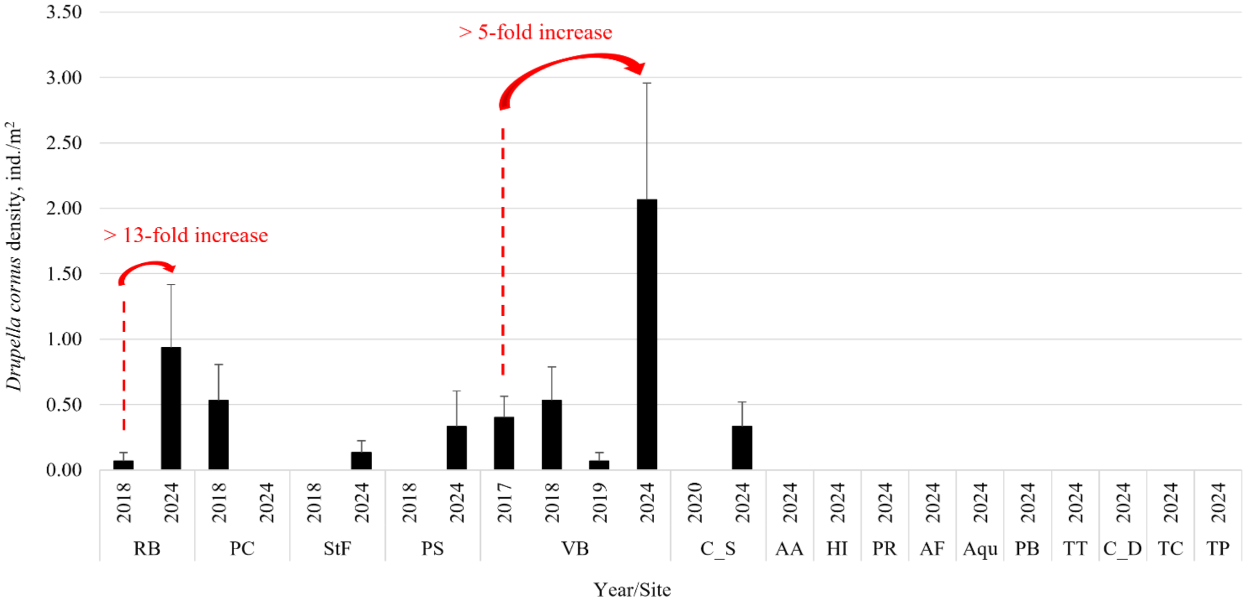

Figure 3. *Drupella cornus* (Röding 1798) density variations from 2017 to 2024 at study sites around Rodrigues. RB: Rivière Banane, PC: Pointe Coton, StF: St François, PS: Passe Semone, VB: Var Brûlée, C_S: Couzoupa_S (shallow waters), AA: Anse Ali, HI: Hermitage Island, PR: Paté Reynieux, AF: Antonio’s Finger, Aqu: Aquarium, PB: Plateau Bénitier, TT: Ti Trou, C_D: Couzoupa_D (dive site), TC: Tombant Coco, and TP: Ti Pate

Turner (1994) suggested that both anthropogenic factors, such as increased terrestrial runoff, overfishing, and reef damage, and natural factors like variable larval recruitment may drive *Drupella* outbreaks. These factors may also contribute to spatial and temporal variations in *Drupella* densities, as changing environmental conditions and reduced predator populations can influence recruitment success and survival. Similarly, Haslam et al. (2025) revealed high genetic connectivity among *D. cornus* populations along the Western Australian coast, indicating they are not genetically distinct. This suggests that larval dispersal plays a significant role in the spread of *Drupella* across regions, potentially leading to outbreaks in new areas. Such connectivity may facilitate rapid colonization of reefs following disturbances, underscoring the importance of understanding genetic flow when managing *Drupella* densities and mitigating their impact on coral reef ecosystems.

Drupella densities recorded align closely with what are considered typical background levels on the Great Barrier Reef, where densities generally remain low, often below 2 ind/m² (Cumming 2009). While these figures are relatively low compared to the severe outbreaks documented elsewhere, they are noteworthy given the potential for *Drupella* to contribute to coral stress, especially on already compromised reefs. In contrast, other regions have experienced far more devastating outbreaks. An estimated population of approximately 500 million individuals was reported in the Ningaloo Marine Park of Australia in 1983 (Ayling and Ayling 1987). A rapid rise in *D. cornus* numbers led to a 75% loss of live coral cover in the back-reef areas of the Ningaloo Reef in the 1980s and 1990s (Turner 1994). In the southwest Indian Ocean, Kaullysing et al. (2016, 2017) reported *Drupella* sp. outbreaks around the island of Mauritius from 2010 to 2014, and in 2016 an outbreak density of 158.14 ± 13.85 ind/m^2 was reported.

The ecological implications of these trends at these sites in Rodrigues could potentially be pointing to environmental stressors affecting coral reefs, such as climate change and coral bleaching or the decline of natural predators, which may have caused *D. cornus* populations to increase (Zhang et al. 2024). The increasing trend may have been driven by reduced corallivore predator pressure, predator removal and/or increased nutrient loading from coastal or agricultural runoff, promoting algal growth and supporting *Drupella* proliferation (Kaullysing et al. 2016; Zhang et al. 2024). As documented by Kaullysing et al. (2016), increased nutrient flow from riverine and coastal runoff promotes macroalgal growth when conditions are favorable leading to the smothering and stress of coral colonies. This makes the corals more susceptible to increased predation by *D. cornus* (Zhang et al. 2024). Excessive input of nutrients in the coastal region may also lead to coral bleaching, further stressing the corals and allowing *D. cornus* densities to increase.

In contrast, some reef sites experienced a decline in *D. cornus* density, such as Pointe Coton, where the population dropped from a relatively high density of 0.53 ± 0.27 ind/m^2 in 2018 to nil observations in 2024, possibly indicating localized environmental recovery, changes in coral health, reduced stress by anthropogenic activities, or natural predation effects. During the surveys at Pointe Coton, live hard coral cover was estimated at 15% in 2018 and 5% in 2024 (personal observations). The abundance of corallivorous gastropods may be better predicted by the abundance of their predators rather than the availability of their coral prey due to the important trophic interactions predators have on controlling the population of gastropods (Shaver et al. 2020). Natural predators of *D. cornus*, such as durophagous fish species and other marine invertebrates, may have increased in abundance (Roff et al. 2019). Nonetheless, Saponari et al. (2021) observed that the distribution of *Drupella* spp. varied significantly at the reef scale, with the highest densities observed in areas with greater coral cover. The loss of coral cover led to the decrease in *Drupella* spp. population, lowering their impact. Lei et al. (2022) also observed higher densities of *Drupella* spp. in areas with higher coral cover. They also reported considerably lower densities of *Drupella* spp. in areas where their preferred diet was limited. Thus, decrease in live hard coral cover or habitat loss may be considered as one of the major drivers of *D. cornus* population decline. Coral bleaching events have increased in frequency and intensity due to rising sea surface temperatures (Reimer et al. 2024). This can lead to large-scale coral mortality (Hughes et al. 2018). As *D. cornus* preferentially preys on stressed corals (Kaullysing et al. 2016), their initial high density may have been linked to a preceding coral bleaching event at Pointe Coton that provided an ample food source of stressed corals. However, a subsequent decline in coral cover due to continued environmental stress may have resulted in the drop of *D. cornus* density (Lei et al. 2022).

The mean number of *D. cornus* differed significantly across sites ($p < 0.001$) and years ($p < 0.001$). The significant interaction between site and year ($p < 0.01$) suggested that both spatial (site) and temporal (year) factors interact in influencing *D. cornus* densities.

The increase in observed population density of *D. cornus* in 2024 around Rodrigues requires further in-depth ecological investigations to assess whether the predation level is indicative of broader reef degradation. The findings of this study point towards patchy distributions of *D. cornus* instead of large aggregations as reported elsewhere globally. It is noteworthy that the density of gastropods around Rodrigues is significantly lower than the densities observed around Mauritius in 2016 (158.14 ± 13.85 ind/m²) (Kaullysing et al. 2017). This lower density may be due to reduced anthropogenic influences and heavy tourism such as high diving or snorkeling activities on Rodrigues' coral reefs and the greater distance of these reefs from the shore, factors contributing to minimizing stress on the corals (Scott et al. 2017). Altogether, this study emphasizes on the importance of continued monitoring of *D. cornus* populations in Rodrigues, as their dynamics could serve as an indicator of reef health and ecosystem changes. The observed site-specific population increase of *D. cornus* emphasizes the need for strategic and adaptive management strategies at specific sites, for example at Var Brûlée.

Prey preference of *Drupella cornus*

Six shallow sites around Rodrigues Island were found to be impacted by corallivorous gastropod *D. cornus* during the study periods (Figures 4.A-4.F), namely, Rivière Banane, Pointe Coton, St François, Passe Semone, Var Brûlée, and Couzoupa_S. The preferred coral hosts varied with predation observed on numerous hard coral species across the affected sites. In general, *D. cornus* showed a preference for tabular and corymbose *Acropora* spp. This may be largely attributed to the availability of the feeding area, ease of access to coral tissue from the base of the coral, as well as shelter (Kaullysing et al. 2016). *Acropora humilis* (Dana 1846) with branching and closely packed structures was also among the targeted species. These findings corroborate the widely documented association of *Drupella* snails with Acroporids.

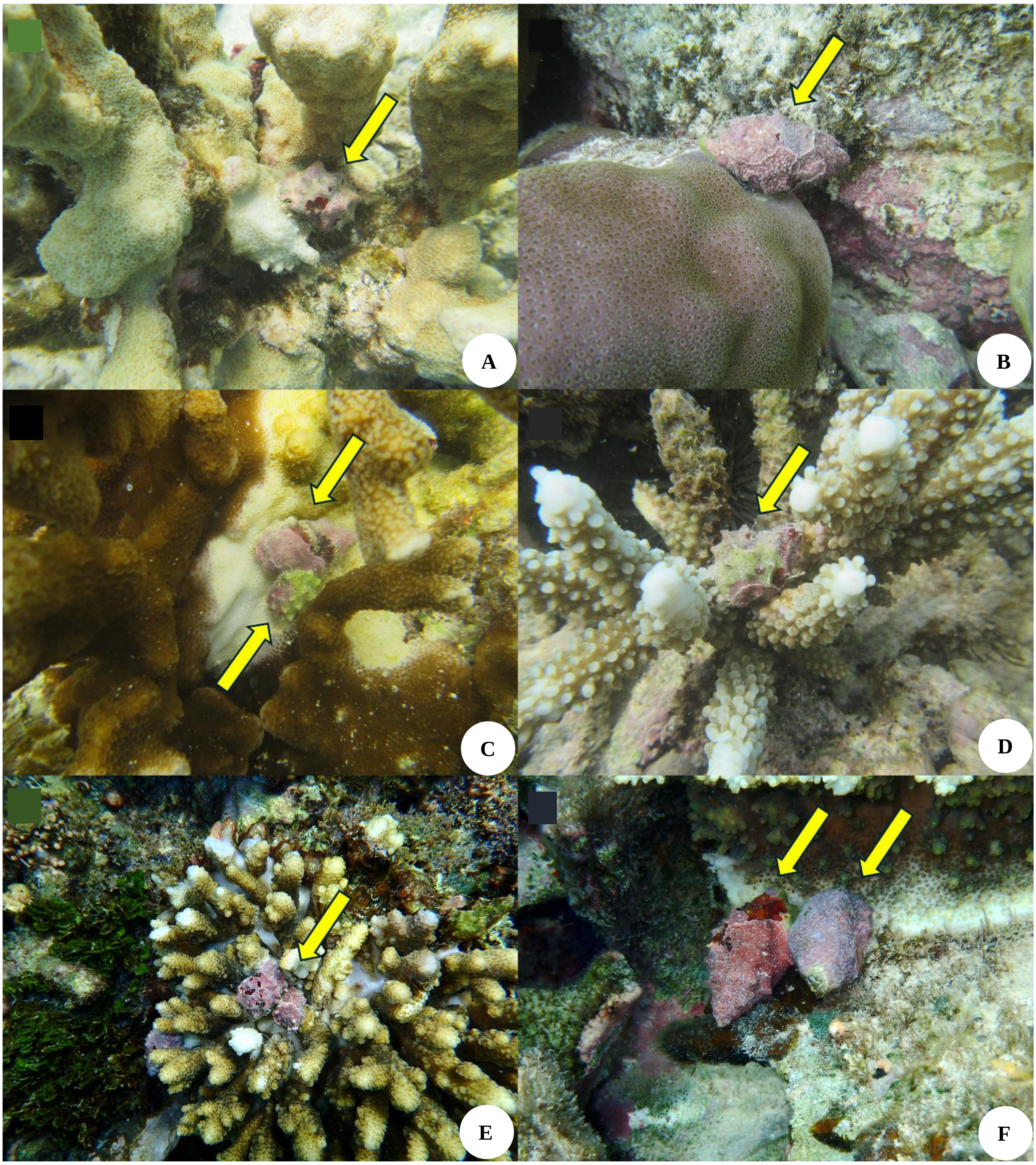

Figure 4. *Drupella* spp. individuals, indicated by yellow arrows, feeding on A. *Montipora* sp. at Var Brûlée in 2017, B. massive *Porites* (Link 1807) at Pointe Coton in 2018, C. *Montipora* (Blainville 1830) at Var Brûlée in 2018, D. *Acropora* sp. at Var Brûlée in 2018, E. corymbose *Acropora* sp. at Var Brûlée in 2024, and F. tabular *Acropora* sp. at Rivière Banane in 2024

Specifically, at Rivière Banane, *D. cornus* was mostly found on tabular *Acropora* as well as in crevices of dead corals, which indicate that these gastropods find shelter in microhabitats for protection from predators (Cumming 2009) or for laying their eggs (Koido et al. 2017; Sam et al. 2017; Kaullysing et al. 2020). At Pointe Coton, *D. cornus* was spotted on corymbose *Acropora* sp., *Pocillopora eydouxi* and on massive *Porites*. Occurrence of *D. cornus* on massive *Porites* Link, 1807 indicates that these gastropods may sometimes occupy less-preferred coral hosts. At St François and Passe Semone, *D. cornus* was seen on tabular *Acropora*, while at Var Brûlée, it was found on *Montipora* sp. and tabular, branching and corymbose *Acropora*. *Pocillopora eydouxi*, massive *Porites* sp., and *Montipora* sp. exhibited lower levels of predation compared to the *Acropora* species. The presence of *D. cornus* on *Montipora* sp. suggests a behavior of opportunistic feeding, likely influenced by coral availability (Cumming 2009). At Couzoupa_S, *D. cornus* was associated with branching *Acropora*.

The prey preference of *Drupella* spp. exhibits dietary plasticity according to the abundance and availability of their favorite coral prey, as well as the "encounter probability" between them (Lei et al. 2022). The observations from the surveys carried out around Rodrigues are in line with prey preference observations through prey choice experiments by Al-Horani et al. (2011), and field observations by Kaullysing et al. (2016, 2017) and Lei et al. (2022), among others, where Acroporids were found to be the preferred diet of *Drupella* spp. Acroporidae has high protein and energy content compared to other coral families (Keesing 1990), thus offering both nutritional benefits and shelter to *D. cornus*.

In conclusion, the lack of observed crown-of-thorns starfish across all surveyed sites in Rodrigues suggested relatively stable reef conditions. However, the presence of suspected COTS feeding scars highlights the need for continued monitoring to confirm whether COTS are present at low densities. In contrast, *D. cornus* was observed at multiple sites, with significant spatio-temporal variations in density, potentially linked to environmental stressors, coral degradation, or predator declines. Therefore, the study revealed that *D. cornus*, rather than COTS, posed a potential threat to Rodrigues reefs, particularly at Var Brûlée and Rivière Banane which can be considered as potential priority reef zones for intervention. The species exhibited a preference for *Acropora* spp. aligning with previous studies on *Drupella* feeding behavior. The preference of *D. cornus* for *Acropora* as prey highlights the potential susceptibility of these corals to *D. cornus* outbreaks, especially in reefs already affected by environmental stressors. Understanding these prey preferences is crucial for monitoring reef health and managing coral predator outbreaks to mitigate their ecological impact. Annual monitoring of *D. cornus* densities is recommended, particularly in shallow reef habitats, and the manual removal of gastropods can be considered once densities exceed 2 ind/m^2. Culling or removing corallivores has been shown to enhance short-term coral recovery, especially when thermal stress is low to moderate, corals have lower heat sensitivity, and corallivore recruitment rates are high (Rogers and Plagányi 2022). Continued monitoring is warranted to ensure early detection in the event that environmental conditions change, but the current results of this study offer an encouraging snapshot of reef stability in Rodrigues in terms of corallivory by COTS and gastropods as none of the values, in terms of spatial distribution, indicate alarming densities so far. Particularly during coral bleaching events, increased monitoring and surveys of corallivores should be carried out as stressed corals are the most susceptible to predation, leading to reduced coral reef health and resilience.

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Coral diseases and associated photosynthetic responses around Rodrigues Island, Western Indian Ocean

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Abstract. *Jogee SY, Anasamy M, Jeetun S, Ricot M, Ramkalam M, Korimbocus A, Kaullysing D, Nascimento B, Casareto BE, Suzuki Y, Wijayanti DP, Bhagooli R. 2025. Coral diseases and associated photosynthetic responses around Rodrigues Island, Western Indian Ocean. Indo Pac J Ocean Life 9: 100-110.* The coral reefs of Rodrigues Island are among the most biodiverse ecosystems in the Western Indian Ocean (WIO) but are increasingly threatened by coral diseases. While disease prevalence has been documented, its physiological impacts remain poorly understood. This study assessed the photo-physiological responses of four reef-building coral species (*Montipora* sp., *Platygyra* sp., *Acropora* sp., *Favia* sp.) affected by Black Band Disease (BBD), Skeletal Eroding Band (SEB), White Band (WB), and White Syndrome (WS). Coral fragments containing both diseased and visually healthy tissues were collected from four sites and analyzed in situ using a Junior-Pulse-Amplitude-Modulated (PAM) fluorometer. Parameters measured included maximum quantum yield (Fv/Fm), maximum relative electron transport rate (rETRmax), maximum non-photochemical quenching (NPQmax), initial slope before saturation (α), post-saturation slope (β), and minimum saturating irradiance (Ik), derived from rapid light curves. Diseased tissues generally exhibited reduced photosynthetic performance, with BBD in *Montipora* sp. and SEB in *Favia* sp. showing the most pronounced declines in Fv/Fm and α, along with altered β and NPQmax values. In contrast, WB and WS had limited or non-significant effects on the measured parameters. These results highlight disease and species-specific vulnerabilities, indicating that some coral-algal symbioses are more susceptible to functional impairment. In the context of climate change, disease-driven stress could accelerate reef degradation, especially in isolated islands like Rodrigues. Integrating photo-physiological monitoring into routine reef health surveys can enhance early detection of functional decline, guide species-targeted restoration, and strengthen adaptive management strategies to safeguard the resilience of Rodrigues' reefs and other WIO coral ecosystems.

Keywords: Chlorophyll fluorescence, coral disease, PAM, photo-physiology, Rodrigues Island, species-specific vulnerability

Abbreviations: α: Alpha (initial slope before the onset of saturation), β: Beta (slope after the onset of saturation), ANOVA: Analysis of Variance, BBD: Black Band Disease, Fv/Fm: F_0: Minimum or Baseline Fluoresence, F_m: Maximum Fluoresence, Maximum Quantum Yield, I_k: Minimum saturating irradiance, NPQ_{max}: Maximum Non-Photochemical Quenching, PAM: Pulse Amplitude Modulation, PAR: Photosynthetically Active Radiation, PWPS: Porites White Patch Syndrome, RLC: Rapid Light Curve, $rETR_{max}$: Relative Maximum Electron Transport Rate, SEB: Skeletal Eroding Band, SEMPA: South East Marine Protected Area. Small Island Developing States: SIDS, WB: White Band, WIO: Western Indian Ocean, WS: White Syndrome, Φ_{PSII}: Effective Quantum Yield

INTRODUCTION

Coral reefs are among the most biologically diverse and productive ecosystems, providing critical ecological goods and services, including habitats for marine biodiversity, shoreline protection, and support for fisheries and tourism, particularly in Small Island Developing States (SIDS) (Hughes et al. 2017; McClanahan et al. 2023). However, coral reefs face numerous global and local stressors, including climate change, ocean acidification, coastal development, overfishing, and coral diseases, which are emerging as significant threats to reef health worldwide (Howells et al. 2020; Good and Bahr 2021; Vega-Thurber et al. 2020). Coral diseases represent a prominent and lethal or sub-lethal threat to coral reef ecosystems globally, contributing to rapid and large-scale coral mortality, biodiversity loss, and ecosystem degradation, with outbreaks documented in various reef systems (Neely and Lewis 2021; Burke et al. 2023). Over the past decade, coral disease incidence has risen sharply, driving substantial declines in reef-building coral populations (Precht et al.

2016; Costa et al. 2021). Understanding the physiological impacts of coral diseases is crucial to assessing their effects on coral resilience and reef stability. Rodrigues Island, situated 600 km east of Mauritius, recently reported multiple coral diseases (Jogee et al. 2023b), yet no research has examined how these diseases affect coral physiology. Rodrigues Island harbors diverse coral communities within its extensive lagoon and fringing reef system but remains highly vulnerable to virulent coral diseases, climate change, and local anthropogenic stressors. While coral bleaching events have been reported in the region (Hardman et al. 2004, 2007), the physiological impacts of coral diseases remain completely unexplored.

Studies on coral diseases primarily focus on field-based identification, prevalence, and distribution patterns (Work and Meteyer 2014). However, fewer investigations have explored the photo-physiological impacts of these factors, which influence coral health and energy acquisition (Lawrence et al. 2015; Grottoli et al. 2018). Coral-algal symbiosis, particularly through the photosynthetic zooxanthellae, is essential for coral survival, as it provides energy through photosynthesis. Disruptions in this relationship, such as those caused by coral diseases, can significantly impair coral function (Higuchi et al. 2015; Suzuki et al. 2015; McClanahan et al. 2023). Pulse-amplitude modulated (PAM) fluorometry is a non-invasive technique widely used to assess photosynthetic performance in corals, including their responses to disease-related stress (Ralph et al. 2015; Bhagooli et al. 2021a).

Previous studies using PAM fluorometry have reported compromised photo-physiology in diseased corals, including reduced maximum quantum yield (Fv/Fm) and lower relative electron transport rates (rETRmax) near disease lesions (Mattan-Moorgawa et al. 2017; Jogee et al. 2023a). For instance, Roff et al. (2008) examined corals affected by White Syndrome, Brown Band, and Skeletal Eroding Band on the Great Barrier Reef, reporting spatial variations in photosynthetic impairment. Burns et al. (2013) documented reduced Fv/Fm in corals with growth anomalies, while Mattan-Moorgawa et al. (2017) found decreased effective quantum yield (ΦPSII) and ETRmax in White Band disease on *Acropora muricata* (Linnaeus, 1758). Similar findings were observed for Black Band, White Band, and Skeletal Eroding Band diseases in Mauritius (Jogee et al. 2023a).

Studies on coral diseases in the Indian Ocean have shown evidence of coral pathologies throughout the region, for example, in the Red Sea (Mohamed and Sweet 2019; Aeby et al. 2021), in the Persian Gulf (Hazraty-Kari et al. 2021; Bharath et al. 2023), in the Atolls of Lakshadweep Islands (Das et al. 2023), in the Republic of Maldives (Bises et al. 2023), and in the Mascarene Islands (Jogee et al. 2023b, 2024). Despite extensive research on coral diseases in the Indo-Pacific, studies in the Western Indian Ocean (WIO)—a region of exceptional coral diversity and endemism—remain limited (McClanahan et al. 2023). Existing WIO research has largely focused on mapping disease prevalence and distribution (Séré et al. 2012, 2015a,b, 2016; Bhagooli et al. 2017, 2021b; Jogee et al. 2023b, 2024), with minimal attention to their physiological impacts. To date, only two studies from Mauritius have assessed photo-physiological responses of diseased corals (Mattan-Moorgawa et al. 2017; Jogee et al. 2023a).

This study addresses this critical knowledge gap by investigating how four prevalent diseases—Black Band Disease (BBD), Skeletal Eroding Band (SEB), White Band (WB), and White Syndrome (WS) affect the photo-physiology of key reef-building corals around Rodrigues Island. Unlike most WIO studies, which focus primarily on disease prevalence and distribution, our approach applies PAM fluorometry, which can proactively detect sub-lethal functional impairment from disease, which often precedes visible tissue loss. PAM fluorometry was used to quantify changes in Fv/Fm, rETRmax, NPQmax, Alpha, Beta, and Ik between healthy and diseased coral tissues. By revealing species-specific physiological vulnerabilities to disease-related stress, this research advances the understanding of coral disease ecology in the WIO; it provides a foundation for adaptive, targeted management strategies to enhance the resilience of Rodrigues' reefs.

MATERIALS AND METHODS

Coral collection sites

This study was conducted around Rodrigues Island (19.7245° S, 63.4272° E), located approximately 600 km northeast of Mauritius Island in the southwestern Indian Ocean. The volcanic island boasts one of the largest lagoons in the WIO region (Chapman 2000) and is surrounded by approximately 90 km of fringing reefs (Soondur et al. 2023). The island has one of the largest marine protected areas in the Indian Ocean, covering an area of around 43 km², known as the South East Marine Protected Area (SEMPA), along with several marine reserves, including Grand Bassin, Passe Demie, Anse aux Anglais, and Rivière Banane. Diseased coral samples were collected through scuba and snorkeling at four sites around the island, namely, Plateau Bénitier, Var Brulée, Pâté Reynieux, and Hermitage Island (Figure 1). These sites were selected following the previous reports of coral diseases observed there in 2020 by Jogee et al. (2023b). With the exception of Plateau Bénitier, located on the north coast of the island at depths of 5-9 m, all the other sites are found in the south, with depths ranging from 1 to 1.5 m.

Coral disease identification and characterization

Coral diseases were identified in the field through visual surveys and using the "Underwater cards for assessing coral health" by Beeden et al. (2008). The gross morphological features of the coral disease-associated lesions were recorded and classified according to the framework proposed by Work and Aeby (2006). Features included the lesion size, lesion color, shape of the lesion, distribution of the lesion on the colony, the margins of the lesion, edges of the lesion, relief of the lesion, and texture of the lesions.

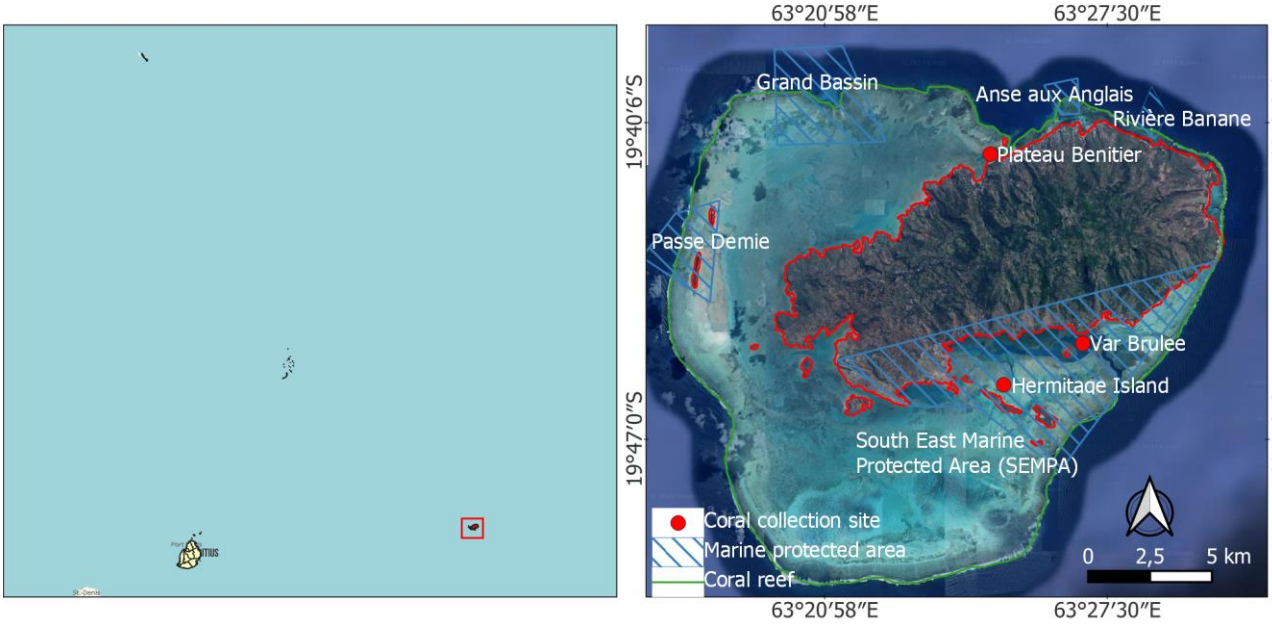

Figure 1. Map of the coral collection sites, marine protected areas, and coral reefs in Rodrigues Island, Mauritius

Photo-physiological assessment

A Junior-Pulse-Amplitude-Modulated (PAM) fluorometer was used to assess the chlorophyll *a* fluorescence of the diseased coral samples collected at various sites around the island. Coral samples were collected using a hammer and chisel or a bone cutter, and the samples were collected in such a way that in included the healthy coral part, the disease lesion part, and the dead and algae-covered part. Coral samples were collected under the Rodrigues Regional Assembly (RRA) Commission for Agriculture, Environment, Forestry, Fisheries, and Marine Parks permit. Measurements were taken at the healthy-looking coral part far (>2-5 cm) from the disease lesion and near (<1 cm) to the disease lesion.

Prior to any PAM measurement using the WinControl Software (v3.34), the coral fragments were dark-adapted for 15 min. The measuring-light intensity was set to between 0.5-1.0 µmol photons m^{-2} s^{-1}, which yielded a stable F_0 without pre-illumination; saturation pulses (~0.8 s) were applied at an intensity of between 3,000-4,000 µmol photons m^{-2} s^{-1} to ensure Fm saturation without overexposure. Rapid Light Curves (RLCs) comprised stepwise actinic PAR increments (0, 66, 90, 125, 190, 285, 420, 625, 845µmol photons m^{-2} s^{-1}; 10-15 s per step), with a saturation pulse at the end of each step. The fluorescence values were zeroed using the F-Offset function, and the gain was brought to 1 prior to taking measurements on a new coral fragment.

The photo-physiological parameters recorded were the Maximum Quantum Yield (Fv/Fm), the maximum relative electron transport rate (rETRmax), and the maximum Non-Photochemical Quenching (NPQ_{max}). A double exponential decay function (Platt et al. 1980) was used to fit curves to the Rapid Light Curves (RLCs) and quantitatively compare the parameters such as α (initial slope of the RLC before the onset of saturation), β (slope after the onset of saturation), I_k (minimum saturating irradiance), and rETRmax (Bhagooli et al. 2021a) between the healthy and diseased coral parts using SigmaPlot software (v.12.0).

Statistical analyses

All statistical analyses were performed at the colony level to compare tissue states (healthy vs near-lesion) within each disease-host combination. Assumptions of normality were assessed using the Shapiro-Wilk test on residuals, and homogeneity of variances was tested using Levene's test. When assumptions of normality or homoscedasticity were violated, data were transformed) before re-testing assumptions. Arcsine square-root transformation was applied since the PAM data are proportion-like values bound between 0 and 1. If assumptions were met, one-way Analysis of Variance (ANOVA) was applied to detect significant differences (α = 0.05) in Fv/Fm, rETRmax, NPQmax, α, β, and Ik among tissue states for each disease-host pairing. All statistical analyses were carried out on R Studio Version 2021.09.0.

RESULTS AND DISCUSSION

Around Rodrigues Island, a total of four coral diseases were observed, identified, and collected for the measurement of their chlorophyll *a* fluorescence. Black Band Disease (BBD) was observed on plating *Montipora* sp. at Var Brulée, located in the south of Rodrigues Island in the SEMPA. BBD in this coral genus was characterized by a thin, narrow, and diffuse black color with undulating annular margins and indistinct edges (Figure 2.A). The lesion was observed on the peripheral part of the coral colony, characterized by tissue loss. The shape of the lesion was irregular, and the edges were indistinct. This disease moderately affected the coral colony, with a range of 25 to 50%. The lesion appeared to be acute due to the presence of a clear, white, denuded coral skeleton, characteristic of recent mortality.

Both the polyp and coenosarc of the coral appeared to be affected by this disease. Although not significant (One-way ANOVA, $p = 0.100$, $F_{1,n} = 3.279$), this might be evident from the much-reduced Fv/Fm values recorded closer to the black band lesion (0.515 ± 0.118) as compared to the healthy-looking coral part (0.620 ± 0.0778) (Figure 3.A). Other observations from key photo-physiological parameters which were not significantly different between the healthy coral part and near the lesion, such as the reduced rETRmax (One-way ANOVA, $p = 0.116$, $F_{1,n} = 3.215$), and α (One-way ANOVA, $p = 0.142$, $F_{1,n} = 2.745$), and the increased NPQmax (One-way ANOVA, $p = 0.794$, $F_{1,n} = 0.072$), and β (One-way ANOVA, $p = 0.071$, $F_{1,n} = 0.307$), might suggest a photo-physiologically compromised health condition near the Black Band lesion on the plating *Montipora* sp. coral, in contrast to the healthy-looking coral parts.

The same disease was also observed to occur on sub-massive *Platygyra* sp. colonies at Plateau Bénitier, located north of Rodrigues Island. The disease in this coral genus was characterized by a large, thick, and black-colored diffuse band that separated the healthy-looking coral tissues from the dead and algae-covered coral skeleton (Figure 2.B). Tissue loss was evident in the region behind the lesion. The lesion was observed on the peripheral part of the colony and had undulating annular margins with distinct edges. Both the polyp and the coenosarc of the coral were observed to be affected as a result of this poly-microbial disease. The shape of the lesion was irregular, and the edges were indistinct. The lesion appeared to be sub-acute due to the absence of a clear, white, denuded coral skeleton, characteristic of recent mortality. A region of algae-covered, dead, and unaffected coral skeleton preceded it. The extent of the disease in this coral genus was severe, with more than 50% of the colony affected. This can be observed from the dissimilarity in the Fv/Fm values between the healthy part of the coral and that near the disease lesion. A significant (One-way ANOVA, $p = 0.047$, $F_{1,n} = 6.904$) drop in the Fv/Fm values (Figure 3.A), which is indicative of reduced photosynthetic capacity, was recorded near the disease lesion (0.469 ± 0.116) compared to the healthy part of the coral colony (0.622 ± 0.0263). Another indication was also evident on the compromised photosynthetic competence of the near lesion coral part as opposed to the healthy coral part from the reduced rETR$_{max}$ values (Figure 2.B), however, all the other photo-physiological parameters including rETRmax (One-way ANOVA, $p = 0.128$, $F_{1,n} = 3.328$), NPQmax (One-way ANOVA, $p = 0.401$, $F_{1,n} = 3.341$), α (One-way ANOVA, $p = 0.115$, $F_{1,n} = 0.65$), β (One-way ANOVA, $p = 0.427$, $F_{1,n} = 3.721$) and Ik (One-way ANOVA, $p = 0.545$, $F_{1,n} = 5.978$) were found to be non-significantly (Tables 1 and 2) different between the healthy coral part and the coral part near the disease lesion.

Skeletal Eroding Band disease was also observed on a *Favia* sp. colony at the same site, Plateau Bénitier, in the north of Rodrigues Island. The disease was characterized by a thin, dark grey line with undulating and indistinct margins, located at the epicenter of the coral colony and separating the healthy-looking tissues from the dead, algae-covered, but slightly eroded coral skeleton (Figure 2.C). Tissue loss was evident from the zone preceding the band. The extent of this disease was moderate, as slightly more than 25%, but less than 50%, of the colony was affected. The mortality associated with this disease was also acute, as evidenced by the white denuded coral skeleton, which is a sign of recent mortality. The shape of the large lesion was irregular, and the polyp, coenosarc, and skeleton appeared to be impacted directly or indirectly by the disease. The impact on all coral features can explain the significantly reduced Fv/Fm values (One-way ANOVA, $p < 0.001$, $F_{1,n} = 205.894$) recorded near the coral lesion (0.482 ± 0.0221) compared to the healthy-looking coral parts (0.652 ± 0.0452). Significantly reduced alpha values (One-way ANOVA, $p = 0.01$, $F_{1,n} = 21.654$) near the disease lesion (0.206 ± 0.0123) compared to the healthy coral part (0.253 ± 0.0126) is an obvious indicator of reduced or compromised photosynthetic performance closer to the disease site (Tables 1 and 2). NPQmax was significantly higher (One-way ANOVA, $p = 0.028$, $F_{1,n} = 16.208$) in the healthy part (0.647 ± 0.084) compared to near the lesion (0.316 ± 0.101). Significantly higher beta values (One-way ANOVA, $p = 0.003$, $F_{1,n} = 40.197$) were also recorded near the disease lesion (0.425 ± 0.001) compared to the healthy parts of the coral 0.0130 ± 0.001. No significant differences were observed in rETRmax (One-way ANOVA, $p = 0.199$, $F_{1,n} = 2.359$) and Ik values (One-way ANOVA, $p = 0.338$, $F_{1,n} = 0.592$).

At the same site, another disease, known as White Band disease, was observed on a branching *Acropora* sp. colony. This disease was characterized by a completely diffuse, white, and denuded band of coral skeleton, which separated the healthy-looking coral from the dead, algae-covered coral skeleton (Figure 2.D). The lesion was wide and located at the basal part of the colony. The lesion margins were smooth, and the edges were distinct with a linear shape. The extent of the disease was mild, as less than 25% of the colony was affected; however, the disease was acute, particularly in the recently exposed denuded coral skeleton. The skeleton at the lesion did not appear to be affected. However, the white color of the skeleton might indicate the loss of the polyp and the coenosarc. However, the data on the photo-physiology of this disease, recorded at Rodrigues Island, do not indicate any statistically significant alteration (Tables 1 and 2) in the photosynthetic capacity of the coral near the disease lesion compared to the healthy coral parts. Fv/Fm was nearly identical between healthy (0.652 ± 0.045) and near-lesion tissue (0.653 ± 0.052) (One-way ANOVA, $p = 0.980$, $F_{1,n} = 0.00$). rETRmax increased slightly from (37.56 ± 24.75) to (45.36 ± 7.52) ($p = 0.478$, $F_{1,n} = 0.55$). NPQmax decreased from (0.582 ± 0.148) to (0.516 ± 0.069). One-way ANOVA, ($p = 0.422$, $F_{1,n} = 0.73$). α increased from (0.123 ± 0.070) to (0.155 ± 0.037) (One-way ANOVA, $p = 0.486$, $F_{1,n} = 0.71$). β declined from (0.0126 ± 0.0072) to (0.0116 ± 0.0053) (One-way ANOVA, $p = 0.896$, $F_{1,n} = 0.02$). Ik decreased slightly from (317.17 ± 236.97) to (314.39 ± 135.81) (One-way ANOVA, $p = 0.993$, $F_{1,n} = 0.00$).

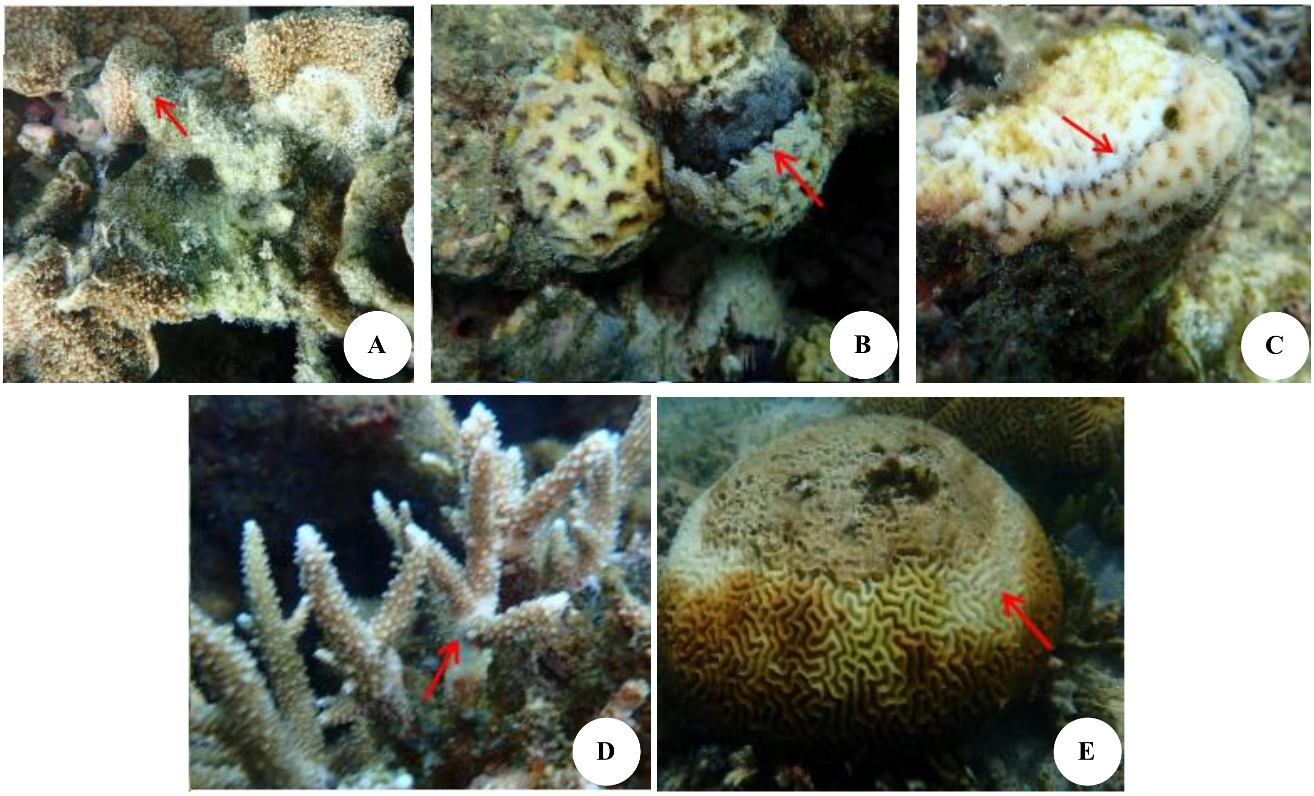

Figure 2. A. Black Band Disease on *Montipora* sp., B. Black Band Disease on *Platygyra* sp., C. Skeletal Eroding Band on *Favia* sp., D. White Band on *Acropora* sp., E. White Syndrome on *Platygyra* sp. (Red arrow shows the location of the disease)

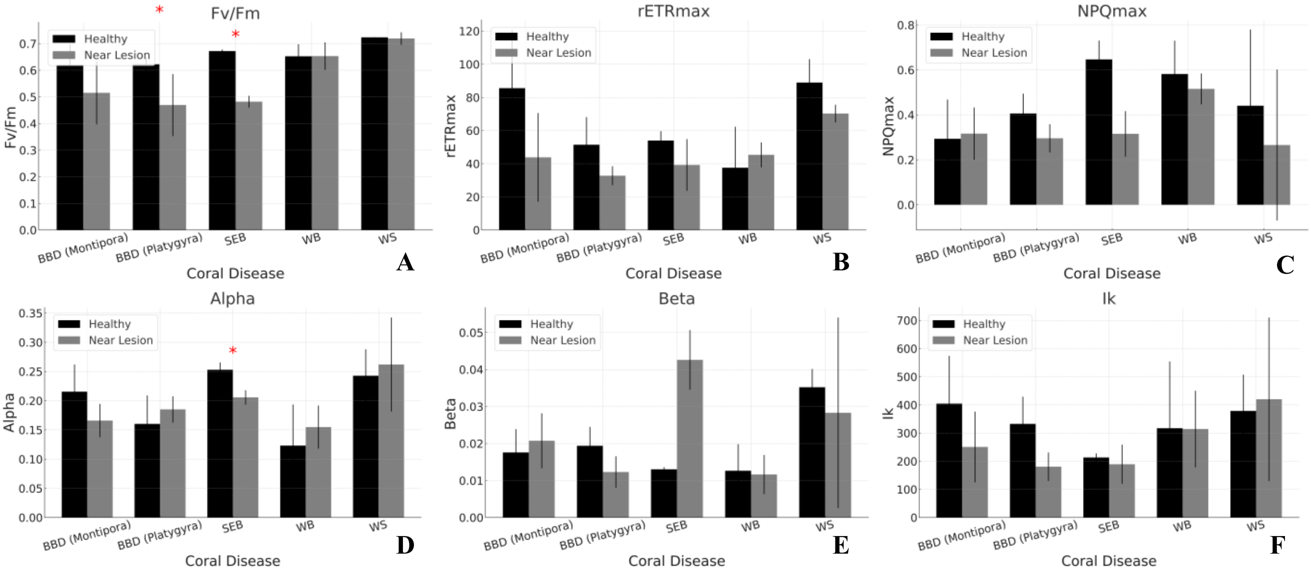

Figure 3. Variation in six photo-physiological parameters between healthy and near-lesion tissues of corals affected by four disease types around Rodrigues Island. A. Maximum quantum yield (Fv/Fm), B. Maximum relative electron transport rate (rETRmax), C. Maximum non-photochemical quenching (NPQmax), D. Initial slope before saturation (α), E. Slope after saturation (β), and F. Minimum saturating irradiance (Ik). Bars represent means ± standard deviation. Red asterisks indicate significant differences between tissue states within a disease-host combination (one-way ANOVA, * - $p < 0.05$). Disease abbreviations: BBD: Black Band Disease, SEB: Skeletal Eroding Band, WB: White Band, WS: White Syndrome

Table 1. Summary of photo-physiological responses of reef-building corals to four coral disease types around Rodrigues Island. Arrows indicate the direction of change in the near-lesion tissue relative to healthy tissue (↓ = decrease, ↑ = increase, - = no directional trend). "ns" denotes non-significant differences ($p > 0.05$). Significant changes ($p < 0.05$) from one-way ANOVA are listed in the final column

Disease type	Host species	Fv/Fm change	rETRmax change	NPQmax change	α change	β change	Ik change	Significant differences ($p < 0.05$)
BBD	*Montipora* sp.	↓ (ns)	↓ (ns)	- (ns)	↓ (ns)	- (ns)	- (ns)	None
BBD	*Platygyra* sp.	↓	↓ (ns)	↑ (ns)	- (ns)	- (ns)	↓ ($p = 0.058$)	Fv/Fm ↓
SEB	*Favia* sp.	↓	- (ns)	↑ ($p = 0.0275$)	↓ ($p < 0.01$)	↑ ($p < 0.01$)	- (ns)	Fv/Fm ↓, α ↓, β ↑, NPQmax ↑
WB	*Acropora* sp.	- (ns)	- (ns)	- (ns)	- (ns)	- (ns)	- (ns)	None
WS	*Platygyra* sp.	↓ (ns)	↓ ($p = 0.0626$)	- (ns)	- (ns)	- (ns)	- (ns)	None

Table 2. One-way ANOVA result of differences in Fv/Fm, $\mathrm{rETR}_{\mathrm{max}}$, $\mathrm{NPQ}_{\mathrm{max}}$, Alpha, Beta, and I_{k} between the healthy part of the coral and near the lesion of Black Band Disease on *Montipora* sp., Black Band Disease on *Platygyra* sp., Skeletal Eroding Band, White Band, and White Syndrome (* - $p < 0.1$, ** - $p < 0.01$, *** - $p < 0.001$)

	Photo-physiological parameters	df	Sum of Squares	F value	*p* value
Black Band Disease on *Montipora* sp.	Fv/Fm	1	0.03287	3.279	0.100
	$\mathrm{rETR}_{\mathrm{max}}$	1	3479	3.215	0.116
	$\mathrm{NPQ}_{\mathrm{max}}$	1	0.00158	0.072	0.794
	α	1	0.004904	2.745	0.142
	β	1	$1.344\mathrm{x}10^{-5}$	0.307	0.609
	I_{k}	1	47311	1.886	0.212
Black Band Disease on *Platygyra* sp.	Fv/Fm	1	0.04022	6.904	0.0467 *
	$\mathrm{rETR}_{\mathrm{max}}$	1	597.9	3.328	0.128
	$\mathrm{NPQ}_{\mathrm{max}}$	1	0.02088	3.341	0.127
	α	1	0.001059	0.650	0.457
	β	1	$8.581\mathrm{x}10^{-5}$	3.721	0.112
	I_{k}	1	39593	5.978	0.0583
Skeletal Eroding Band	Fv/Fm	1	0.05415	205.9	0.0137 *
	$\mathrm{rETR}_{\mathrm{max}}$	1	324.9	2.359	0.199
	$\mathrm{NPQ}_{\mathrm{max}}$	1	0.13134	16.21	0.0275*
	α	1	0.003351	21.65	0.0464 *
	β	1	0.0013113	40.200	0.0317 *
	I_{k}	1	848	0.338	0.592
White Band	Fv/Fm	1	0.000001	0.00	0.987
	$\mathrm{rETR}_{\mathrm{max}}$	1	91.2	0.273	0.629
	$\mathrm{NPQ}_{\mathrm{max}}$	1	0.00658	0.492	0.522
	α	1	0.001511	0.478	0.527
	β	1	0.0000015	0.038	0.856
	I_{k}	1	12	0.00	0.987
White Syndrome	Fv/Fm	1	0.0000241	0.058	0.821
	$\mathrm{rETR}_{\mathrm{max}}$	1	465.4	6.558	0.0626
	$\mathrm{NPQ}_{\mathrm{max}}$	1	0.0366	0.323	0.610
	α	1	0.000493	0.092	0.777
	β	1	0.0000635	0.126	0.740
	I_{k}	1	2068	0.034	0.866

White Syndromes were observed at two sites in the south of Rodrigues Island in the SEMPA, Hermitage Island, and Pâté Reynieux. This disease was observed primarily on massive *Platygyra* sp. colonies. This disease was characterized by large, diffuse, and oblong areas of tissue loss with focal to multifocal and coalescing distribution (Figure 2.E). Most of the observed lesions occurred at the colony-wide level and were not restricted to a specific part of the affected colony. Areas of dead coral skeletons covered with algae were observed in the center of the lesions. The edges of the lesion were smooth, and the margins were distinct. Most of the colonies were moderately to severely affected by the White Syndromes. The loss of polyp and coenosarc was evident from the bare white coral skeleton. Tissue loss was acute to sub-acute, as evidenced by the large areas of denuded and algae-free coral skeleton. Although there are some indications that the White Syndromes compromise the photo-physiology of the affected coral, as observed from the slight reduction in Fv/Fm and $rETR_{max}$ values (Figure 3.A), the extensively observed disease around these two sites does not show any significant variation ($p < 0.05$) (Tables 1 and 2) in any of the photo-physiological parameters between the healthy part of the coral and near the disease lesion. Fv/Fm declined slightly from (0.724 ± 0.001) to (0.719 ± 0.023), (One-way ANOVA, p = 0.553, $F_{1,n}$ = 0.40). rETRmax decreased from (88.93 ± 14.12) to (70.25 ± 5.31) (One-way ANOVA p = 0.0626, $F_{1,n}$ = 6.07). NPQmax declined from (0.441 ± 0.339) to (0.266 ± 0.336) (One-way ANOVA p = 0.400, $F_{1,n}$ = 0.79). α increased from (0.243 ± 0.045) to (0.262 ± 0.080) (One-way ANOVA, p = 0.682, $F_{1,n}$ = 0.19). β declined from (0.0352 ± 0.0050) to (0.0283 ± 0.0258) (One-way ANOVA p = 0.474, $F_{1,n}$ = 0.60). Ik increased from (378.37 ± 128.82) to (419.89 ± 290.28) (One-way ANOVA, p = 0.757, $F_{1,n}$ = 0.10).

Discussion

The morphological diagnosis of Black Band Disease on the plating *Montipora* sp. coral aligns with the observations of several other studies (Aeby et al. 2015; Chen et al. 2017; Das et al. 2022). This disease has been previously reported in *Montipora* at various locations worldwide (Aeby et al. 2015; Chen et al. 2017; Das et al. 2022). Although the results of the photo-physiology of the Black Band Disease on *Montipora* sp. did not show any significant difference between the healthy part of the affected coral colony and near the actual disease lesion, declines in parameters such as Fv/Fm and $rETR_{max}$ indicate some level of compromised photo-physiological performance near the lesion compared to the healthy coral part. This observation aligns with that of Roff et al. (2008), who reported reduced Fv/Fm and rETRmax values closer to the Black Band Disease lesion in *Cyphastrea microphthalma* (Lamarck, 1816). However, the same study also highlighted the strong spatial variation and heterogeneity in the photo-physiology of this particular coral disease. This might explain the non-significant differences observed in the photo-physiological parameters between the healthy part and near the disease lesion. Chlorophyll *a* fluorescence should have been recorded at a much finer spatial scale, on the order of mm, as in Roff et al. (2008), in order to accurately decipher variations in the photo-physiology of the Black Band Disease across the coral colony. The reduction in Fv/Fm or $rETR_{max}$ can be attributed to the highly anaerobic and sulfide-rich micro-environment that exists closer to the Black Band (Sato et al. 2017). In addition to the lack of finer spatial resolution for chlorophyll *a* fluorescence measured in this study for the Black Band Disease, the lack of significant difference between the photo-physiology of the healthy part of the coral and that near the disease lesion can be explained by the presence of photosynthetic activities (Sato et al. 2016) close to the lesion by one of the causative cyanobacterial pathogens of this disease, *Phormidium corallyticum* (Rützler and Santavy 1983). The presence of cyanobacteria may influence the accurate measurement of chlorophyll fluorescence in the coral. This finding suggests that monitoring for this disease should include fine-scale (mm-level) PAM measurements using Imaging-PAM near BBD fronts to detect early decline.

The Black Band Disease on *Platygyra* sp. has been previously reported on this genus at several sites worldwide (Thinesh et al. 2014; Hadaidi et al. 2018; Aeby et al. 2020; Bharath et al. 2020; Mohamed et al. 2023). Similar to *Montipora* sp., the morphological diagnosis of Black Band Disease on *Platygyra* Ehrenberg, 1834 has been confirmed by multiple studies (Beeden et al. 2008; Hadaidi et al. 2018; Bharath et al. 2020). The lower Fv/Fm values observed near the lesion of the Black Band Disease, as opposed to the healthy part of the coral, match the observation of Roff et al. (2008) and Jogee et al. (2023a), who both reported a decline in Fv/Fm values closer to the Black Band Disease lesion. This drop in the maximum quantum yield can be attributed to the presence of an anaerobic and sulfide-rich environment, caused by the sulfide-oxidizing bacteria *Beggiatoa* spp. (Sato et al. 2017), which is unfavorable for photosynthesis by zooxanthellae inside the coral tissues. This unfavorable condition can also lead to the expulsion of zooxanthellae, as reported for the impact of zooxanthellae exposure to anaerobic conditions (Howard and Schul 2023). This could help explain the reduction in photosynthesis near the Black Band Disease lesion. However, Roff et al. (2008) reported a significant increase in NPQmax values closer to the disease lesion, whereas our observation showed no such trend. This may be attributed to significantly coarser spatial resolution for data collection in this study compared to the above study, or damage to the photosynthetic apparatus of the zooxanthellae. Similarly to the BBD on *Montipora* sp., this finding suggests that monitoring for this disease should include fine-scale (mm-level) PAM measurements using Imaging-PAM near BBD fronts to detect early decline.

The Skeletal Eroding Band disease on *Favia* sp. has been previously reported in this coral genus (Montano et al. 2012) and described with similar morphological characteristics (Beeden et al. 2008; Page and Willis 2008; Montano et al. 2012). Our observation on the reduction of Fv/Fm corroborates that of Jogee et al. (2023a), but not with that of Roff et al. (2008), who observed no variation in Fv/Fm between the healthy part and the disease lesion. Only an increase in $rETR_{max}$ was observed further away from the lesion by Roff et al. (2008). The decline in Fv/Fm values near the disease lesion can be attributed to the loss of the coral tissues along with the photosynthetic zooxanthellae in that part of the coral as a result of the spinning movement of the causative pathogen, *Halofolliculina corallasia*, which embeds itself in the coral skeleton and disrupts the coral tissue. *Halofolliculina corallasia* has also been observed to engulf zooxanthellae cells (Page et al. 2015), which could explain the reduction in Fv/Fm values closer to the disease lesion compared to the healthy-looking coral tissues. Tissue loss also occurs as a consequence of chemical secretions that are produced by the pathogens of the Skeletal Eroding Band disease during the ciliate's loricae formation process (Page et al. 2015). In addition to the loss of coral tissue and zooxanthellae, the ingestion of photosynthetic zooxanthellae cells by pathogenic ciliates has also been observed (Ravindran et al. 2023). The reduction in alpha values observed near the lesion compared to the healthy part of the coral may be explained by the compromised light-harvesting and processing efficiency resulting from the eroded corallite structures and, thus, the compromised light microenvironment. These findings indicate that early detection via PAM fluorometry could inform management actions to prevent widespread disease propagation.

The White Band disease observed on the branching *Acropora* sp. colony at Plateau Bénitier is consistent with the morphological descriptions provided in multiple studies conducted worldwide (Lentz et al. 2011; Ainsworth et al. 2015; Nugraha et al. 2019; Gignoux-Wolfsohn et al. 2020). The observation of the bleaching pattern on the *Acropora* sp. coral associated with the White Band suggests that the disease may be of White Band Type II (Ritchie and Smith 1998). As opposed to a study by Mattan-Moorgawa et al. (2017) and Jogee et al. (2023a), who reported lower effective quantum yield and NPQ_{max} in White Band-affected *A. muricata*, no significant difference ($p > 0.05$) in the photo-physiological parameters was reported between the healthy part of the coral and near the disease lesion. Another possible explanation could be the presence of photosynthetically active and competent coral tissues with zooxanthellae cells in the disease lesion where the measurements were recorded. The remaining zooxanthellae cells might still emit a fluorescence signal. This observation warrants the need for visual monitoring paired with molecular diagnostics to proactively detect sub-lethal infection.

White Syndrome is the general name given to a widespread group of observed lesions that are characterized as white patches, bands, or blotches on generally non-acroporid corals (Bourne and Willis 2015; Cróquer et al. 2021). The morphological characteristics of the observed lesions in this study align with those reported by others (Bourne et al. 2015; Howells et al. 2020). This disease has been reported in the *Platygyra* Ehrenberg, 1834 genus by several studies worldwide (Bourne et al. 2015; Muzaki et al. 2017; Raksachon et al. 2017; Howells et al. 2020). White Syndrome is primarily distinguished from other White Diseases by the absence of microbial involvement in the disease progression (Ainsworth et al. 2007). While no photo-physiological assessment has been performed on White Syndromes, observations have been made on White Plague diseases in *A. muricata* and *Porites lobata* Dana, 1846, which have shown contrasting Fv/Fm, rETRmax, and NPQmax values between the near-lesion part of the affected corals and the healthy coral part (Mattan-Moorgawa et al. 2017). This contradicts our findings, which did not reveal any significant differences. However, another study by Roff et al. (2008) on the photophysiology of White Syndrome in *Acropora* made a similar observation to this study, where the tissues near the disease lesion did not appear to be photosynthetically compromised. The explanation of this finding was revealed by the observation of structurally intact zooxanthellae cells with no signs of degradation at the disease lesions (Roff et al. 2008). This might explain our observation of no significant difference in any of the photo-physiological parameters investigated in this study between the healthy part of the coral and the area near the disease lesions in White Syndrome-affected coral colonies. Given the potential for this disease to persist without measurable photosynthetic impairment, management should combine visual prevalence surveys with histological or molecular assays.

Across the diseases investigated, BBD and SEB produced clear and statistically significant declines in photo-physiological performance, particularly Fv/Fm, whereas WB and WS did not show measurable impairment despite visible lesions. This divergence likely reflects fundamental differences in pathogen biology and disease mechanisms. BBD and SEB are driven by active microbial pathogens with direct, destructive interactions with coral tissues and their symbiotic algae. In BBD, the polymicrobial consortium—dominated by cyanobacteria (*Phormidium corallyticum*) and sulfide-oxidizing bacteria (*Beggiatoa* spp.)—creates a hypoxic, sulfide-rich microenvironment at the lesion front (Rützler and Santavy 1983; Sato et al. 2017), which is toxic to zooxanthellae and impairs photosynthetic electron transport. In SEB, the ciliate *Halofolliculina corallasia* physically bores into coral skeletons and ingests zooxanthellae cells (Page et al. 2015; Ravindran et al. 2023), leading to direct loss of photosynthetic tissue. Both diseases, therefore, result in immediate and severe disruption of coral-algal symbiosis and light-harvesting efficiency, producing measurable declines in chlorophyll fluorescence metrics. In contrast, WB and WS lesions did not exhibit significant changes in Fv/Fm, *rETRmax*, or other PAM parameters. For WB Type II, although pathogenic bacteria are suspected (Ritchie and Smith 1998), the lesion margins in this study contained photosynthetically competent tissues, suggesting that the rate of tissue loss may not yet have impaired algal photochemistry. WS, on the other hand, lacks a confirmed microbial pathogen (Ainsworth et al. 2007) and may result from abiotic stressors or secondary colonization of already stressed tissue, allowing zooxanthellae within lesion-adjacent tissues to remain intact and photosynthetically active (Roff et al. 2008). This would explain the maintenance of chlorophyll fluorescence despite visible tissue loss or discoloration. The pronounced differences in physiological impact observed here highlight the importance of integrating pathogen biology into coral disease diagnostics. Microbially mediated diseases such as BBD and SEB produce predictable and rapid declines in photo-physiology, while non-microbial or less aggressive etiologies may leave photosynthetic parameters unaffected until later stages. Recognizing these distinctions is crucial for designing targeted monitoring protocols, selecting early-warning indicators, and prioritizing management interventions.

In conclusion, this study highlights the photo-physiological impacts of coral diseases on reef-building corals around Rodrigues Island, with significant reductions in Fv/Fm for Black Band Disease and Skeletal Eroding Band. While some diseases showed no major physiological effects, limitations in measurement resolution were noted. The identification and monitoring of the progression rates of high-impact diseases and their associated physiological signatures can guide prioritization of intervention sites. The findings of this study support the adoption of a tiered approach: (i) standardized lesion classification (Beeden et al. 2008; Work and Aeby 2008) for field surveys; (ii) targeted PAM fluorometry at lesion margins for early detection of functional decline; and (iii) integration of environmental monitoring (temperature, light, turbidity) to link disease dynamics with environmental drivers. Such an approach will improve temporal resolution, diagnostic accuracy, and comparability of disease data across WIO reef systems. The results of this study can support the design of adaptive management strategies that incorporate disease surveillance into Marine Protected Area (MPA) management plans, guide restoration site selection under national reef recovery programs, and strengthen regional cooperation on coral health monitoring. The findings highlight the vulnerability of key coral species to disease-driven stress and underscore the need for further physiological and microbiological characterization as well as increased temporal and spatial PAM data collection to inform species-specific conservation and adaptive reef management strategies for Rodrigues Island.

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Photo-physiological thermal stress responses of *Echinopora forskaliana* from shaded and light-exposed environments around Rodrigues Island, Western Indian Ocean

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Abstract. *Jeetun S, Ricot M, Jogee SY, Taleb-Hossenkhan N, Ramah S, Perrine JS, Kaullysing D, Bhagooli R. 2025. Photo-physiological thermal stress responses of* Echinopora forskaliana *from shaded and light-exposed environments around Rodrigues Island, Western Indian Ocean. Indo Pac J Ocean Life 9: 111-123.* Corals in shaded and exposed habitats experience variable heat and light stresses, impacting their photosynthetic performance and resilience to thermal stress. This study examined bleaching, photosynthetic performance, and growth patterns of *Echinopora forskaliana* (Milne Edwards & Haime, 1849) in shaded and exposed environments at St. François, Rodrigues Island. Bleaching prevalence and colony sizes were recorded using three belt transects. Field observations in 2018 revealed healthy-looking colonies in shaded habitats, while colonies in exposed habitats showed bleaching. Responses of healthy-looking *E. forskaliana* colonies from both habitats were assessed under exposure to 29 and 32°C. Effective quantum yield at Photosystem II (Φ_{PSII}), maximum relative electron transport rate ($rETR_{max}$), and maximum non-photochemical quenching (NPQ_{max}) were measured at the start, and after 3 and 12 hours of exposure. Field bleaching surveys showed that 93.3% of exposed colonies were pale/bleached, while shaded ones remained unaffected and were significantly larger (42.1±9.0 cm). Thermal stress at 32°C and 206.5±27.0 Lux caused steep declines in Φ_{PSII} (99.7%), $rETR_{max}$ (93.5%), and NPQ_{max} (97.37%) in exposed colonies after 12 hours, while shaded colonies maintained their photosynthetic performance. These findings suggest that shaded habitats may act as refugia for corals under climate-induced thermal stress, highlighting the need for adaptive conservation and management approaches. The urgency of adaptive conservation and management approaches is underscored, as these findings highlight the need for immediate action to protect these crucial habitats.

Keywords: Bleaching susceptibility, climate change, coral, *Echinopora forskaliana*, PAM, Rodrigues, thermal stress

Abbreviations: Φ_{PSII}: Effective Quantum Yield at Photosystem II; $rETR_{max}$: Maximum Relative Electron Transport Rate; NPQ_{max}: Maximum Non-Photochemical Quenching; SST: Sea Surface Temperature; ROS: Reactive Oxygen Species; WIO: Western Indian Ocean

INTRODUCTION

Coral reefs are highly vulnerable to rising sea temperatures, which have increased the frequency and severity of coral bleaching episodes (Hughes et al. 2017; Lough et al. 2018; Sully et al. 2019). These occurrences contribute to reduced coral development and increased mortality (Hughes et al. 2018; Brown et al. 2019; Matsuda et al. 2020). Coral bleaching, induced by environmental stressors such as high sea surface temperatures (SST) and sun radiation, disturbs the coral Symbiodiniaceae symbiosis, essential for coral metabolism (Bieri et al. 2016; Goulet and Goulet 2021). Heat stress affects coral metabolism and lowers the photosynthetic efficiency of their symbiotic microalgae, limiting energy for growth, reproduction, and calcification (Allen-Waller and Barott 2023; Bouwmeester et al. 2023).

Light availability plays a crucial role in coral health, growth, and overall ecological functioning, influencing physiological processes such as photosynthesis, calcification, and symbiont density (Ross et al. 2022). Both excessive low and high light levels can be damaging to corals. While high ultraviolet (UV) radiation exposure can induce photoinhibition and coral tissue damage, insufficient illumination lowers photosynthesis (Falkowski et al. 1993). Especially during midday, exposure to intense light on shallow reefs causes oxidative stress, generates reactive oxygen species (ROS), and leads to photoinhibition (Helgoe et al. 2024; Lesser 2024), resulting in coral bleaching through symbiont loss or damage (Ainsworth and Brown 2021). High irradiance also worsens heat stress effects, making corals more vulnerable to rising temperatures. (Hughes et al. 2017; Courtial et al. 2017; Rosic et al. 2020). Prolonged exposure to elevated SST and intense light can compromise coral defense mechanisms, causing tissue loss, increased disease susceptibility, and eventual mortality, driving reef degradation and biodiversity loss (Riegl and Purkis 2015; Elliot et al. 2018; Muller et al. 2018; McClanahan and Muthiga 2021).

Shading reduces light availability and mitigates bleaching under high temperatures (Baker et al. 2008; Berg et al. 2020; Butcherine et al. 2023). Reduced light environments, such as turbid waters (Cacciapaglia and van Woesik 2015; Morgan et al. 2017; Sully and van Woesik 2020; Rosedy et al. 2023), cloud cover (Gonzalez-Espinosa and Donner 2021), mangrove shading (Stewart et al. 2021), and deeper or sheltered reef zones (Smith et al. 2016; Cowburn et al. 2019), help mitigate stress by providing more moderate lighting conditions. In shaded environments, corals sustain stable photosynthetic rates, lowering oxidative stress and enhancing resistance to UV rays and high temperatures (Ellis et al. 2024). They are less likely to depend on photoprotective processes like non-photochemical quenching (NPQ), enabling them to sustain higher symbiont densities and better growth rates than corals in high light environments (Butcherine et al. 2023). Shaded reefs, especially in deeper or more sheltered areas, act as refuges from thermal and light stress, promoting healthier coral colonies (Stewart et al. 2021). The size and structure of coral colonies can influence how much light they receive and their susceptibility to bleaching. Smaller colonies in exposed areas may experience greater stress and limited growth, while shaded or sheltered corals often show higher survival and resilience (Glynn and D'Croz 1990; Fabricius 2006; Enríquez et al. 2017). Recent work has also examined how varying light conditions, including artificial shading, affect coral physiology and bleaching susceptibility, highlighting the potential of shading technologies for conservation (Tagliafico et al. 2022). In contrast, other studies have also reported potential drawbacks of reduced light availability, noting that increased turbidity can adversely impact coral health (Smith et al. 2016; Fisher et al. 2019; Juhi et al. 2021; López-Londoño et al. 2021; Diaz et al. 2023).

Previous studies from the Western Indian Ocean (WIO) have highlighted the role of thermal refugia in the potential for coral survival. In Mauritius, spatial thermal variability affected bleaching patterns, with bleaching primarily occurring in lagoonal and reef flat areas. At the same time, nearshore colonies exhibited greater thermal resilience despite experiencing higher maximum seawater temperatures. (Bhagooli and Taleb-Hossenkhan 2012). This pattern aligns with studies on *Acropora muricata* (Linnaeus, 1758), demonstrating enhanced photo-physiological responses and antioxidant activity in nearshore environments compared to the lagoon and reef, suggesting a greater thermal stress resilience (Louis et al. 2016, 2020). Other chlorophyll stress studies have indicated variations and stress responses in photo-physiology of corals (Ghoora et al. 2018; Mattan-Moorgawa et al. 2018, 2020; Bhagooli et al. 2021b; Munbodhe et al. 2023, 2025; Jeetun et al. 2023, 2025; Ricot et al. 2023) and other marine symbiotic organisms (Ramah et al. 2023) and seaplants (Bhagooli et al. 2021c; Narrain et al. 2023).

The reefs of the Western Indian Ocean (WIO) region have experienced repeated bleaching events over the years. Variations in thermal regimes have also influenced bleaching patterns, with Mauritius experiencing higher bleaching in 2019 compared to 2016, affecting multiple test species (Jeetun et al. 2025). Rodrigues, another key study site in the WIO, has also experienced repeated bleaching events, first recorded in 2005 (Hardman et al. 2007), and additional stressors, including sedimentation, coral diseases, and destructive fishing practices, have further contributed to reef degradation (Hardman et al. 2004, 2013; Jogee et al. 2023). However, the potential influence of shaded environments on thermal bleaching responses remains unexplored in the WIO.

Despite evidence of the significance of shaded habitats, studies comparing coral responses between shaded and exposed environments in the waters of the Republic of Mauritius remain limited. This study aims to investigate the photo-physiological responses and growth patterns of *Echinopora forskaliana* (Milne Edwards & Haime, 1849) in both shaded and light-exposed environments at St. François, Rodrigues Island. Using pulse-amplitude modulation (PAM) fluorometry, photo-physiological parameters such as effective quantum yield, relative electron transport rate ($rETR_{max}$), and non-photochemical quenching (NPQ_{max}) were examined. In addition, the effects of thermal stress on corals from both environments were evaluated to understand their resilience mechanisms better. By integrating in situ and ex situ assessments, this study is critical for understanding the environmental factors that impact coral functioning and informing conservation strategies for WIO reefs amid climate change.

MATERIALS AND METHODS

Study area

The study was conducted in 2018 at St. François (19°41'56.4"S 63°30'00.5"E), on the east coast of Rodrigues Island, which hosts the most extensive and well-developed reefs in the Mascarenes (Bhagooli and Kaullysing 2019), located in the WIO (Figure 1). A combination of shallow, exposed reef flats and shaded habitats within a natural channel characterizes this site. In the shallow reef flat, at depths of 1 to 1.5 m, *E. forskaliana* corals experience high light intensity and ultraviolet (UV) radiation. Conversely, the natural channel at St. François provides shaded conditions along its vertical walls, where corals are located at depths ranging from 1.5 to 8 m (Figure 2). These shaded habitats are distinguished by lower light intensity due to overhangs and channel structure, which results in lower temperatures compared to the reef flat, as the channel's depth and structure limit direct sunlight and reduce heat exposure.

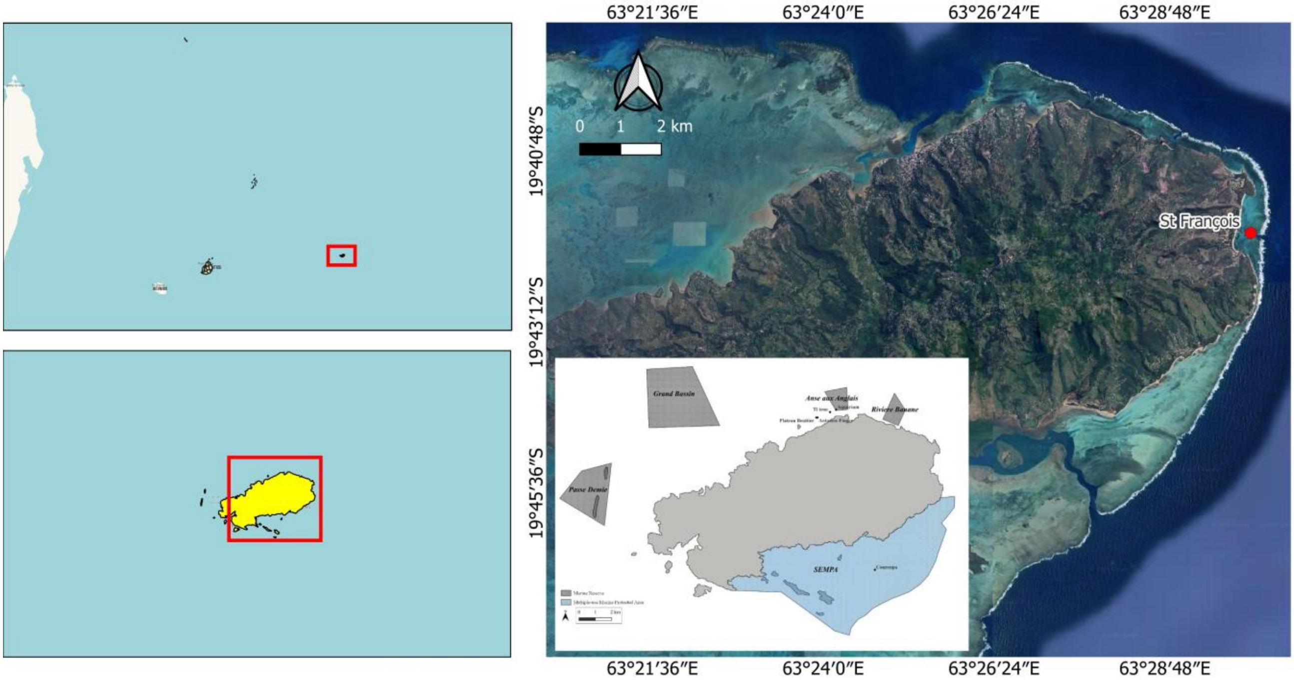

Figure 1. The study site, St. François, is situated on the east coast of Rodrigues Island. The study site features shallow and exposed reef flats and shaded habitats along a natural channel

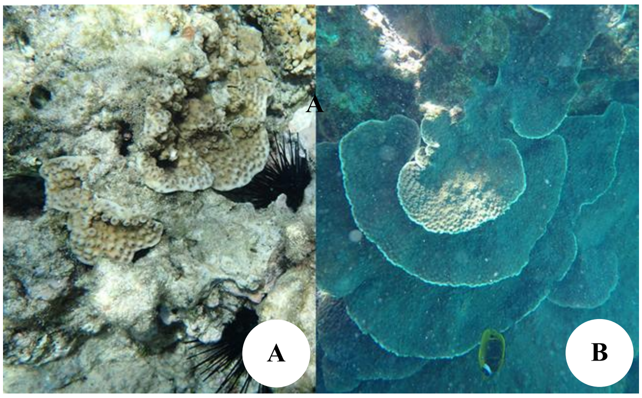

Figure 2. *Echinopora forskaliana* at St. François, Rodrigues Island. A. Exposed to light conditions on the reef flat at a depth of 1- 1.5 m; and B. Shaded from light on the walls of the channel at a depth of 1.5-8 m

This area provides a gradient of both thermal and light exposure that enables a comparative analysis of coral photo-physiological responses and growth patterns under contrasting light and temperature. Temperature and light intensity were measured every 15 minutes in both exposed and shaded areas using HOBO Pendant® Temperature/Light sensors, which were deployed at 1.5 m depth in the exposed reef flat and at 3 m depth along the shaded channel wall. Measurements were recorded continuously during the warm season in April 2018. Light intensity measurements recorded in lux were converted to photosynthetically active radiation (PAR) units of μmol photons m^{-2} s^{-1} using a standard sunlight calibration factor of 0.0185.

Bleaching and colony size survey

A bleaching survey was conducted at St. François, focusing on *E. forskaliana* colonies in shaded and exposed environments. Initial surveys noted pre-existing differences in pigmentation and colony morphology across reef zones, with shaded colonies generally appearing darker and larger than those in exposed environments. These baseline differences were taken into account throughout the study to avoid misclassification of natural variation as bleaching. This approach ensured that observed changes in pigmentation or morphology were attributed to thermal stress responses rather than inherent site-specific traits.

Bleaching magnitude and colony size variations were assessed during summer in 2018. Bleaching observations were carried out across three 100 m^2 (50 × 2 m) belt transects, including exposed reef flats and shaded channel walls. Along each transect, 10 randomly selected *E. forskaliana* colonies were visually assessed for bleaching condition and classified as "Healthy" and "Pale", following the CoralWatch Coral Health Chart (Siebeck et al. 2006). Colony size was measured in situ to the nearest centimeter using a flexible measuring tape. For each colony, the maximum diameter and two perpendicular diameters were recorded to account for irregular shapes and provide a more accurate size estimate.

Chlorophyll fluorescence parameters

To assess the photosynthetic performance and stress responses of *in situ* zooxanthellae, a Diving Pulse-

Amplitude Modulated (D-PAM; WALZ, Germany) fluorometer was used to measure chlorophyll *a* fluorescence, quantum yield (Φ_{PSII}), relative electron transport rate ($rETR_{max}$), and non-photochemical quenching (NPQ_{max}) (Bhagooli et al. 2021a). These parameters are derived from base (F or F_t) and maximum (F_m or F_m') fluorescence measured using a D-PAM fluorometer. The $rETR_{max}$ and NPQ_{max} were derived from the rapid light curves (RLCs) generated by the D-PAM.

The effective quantum yield at PSII, Φ_{PSII} (Genty et al. 1989), quantifies the quantity of light utilized by chlorophyll molecules in photochemistry in the PSII. The following equation was used to determine this parameter:

$$\text{Effective Quantum yield at PSII, } \Phi_{PSII} = \frac{\Delta F}{F_m'} = \frac{F_m' - F_t}{F_m'}$$

Where F_m' is the maximum fluorescence in light-adapted conditions, and F_t is the steady-state fluorescence value prior to the saturating pulse.

The relative electron transport rate (rETR) is a light-adapted parameter that measures the gross photosynthetic activity in vivo (Genty et al. 1989). This is determined as follows:

$$rETR = \Phi_{PSII} \times PAR \times 0.5$$

Where Φ_{PSII} is the effective quantum yield of PSII, PAR is the photosynthetic active radiation (µmol photons m^{-2} s^{-1}), and 0.5 is a partitioning factor which accounts for the energy distribution between PSI and PSII.

Non-photochemical quenching (NPQ) is the mechanism through which photosynthetic organisms convert and dissipate the excess excitation energy into heat at PSII to guard themselves against the negative effects of intense lighting. NPQ is quantified using the following equation:

$$NPQ = \frac{F_m - F_m'}{F_m'}$$

Initial measurements included shaded corals and healthy-looking and bleached corals from the exposed habitat. The experiment focused on shaded corals and healthy-looking exposed corals, comparing their responses under controlled temperature treatments.

Field sampling and initial photo-physiological measurements

Field observations indicated differences in coral condition between habitats, which determined fragment selection for subsequent measurements and experiments. To assess initial *in situ* photo-physiological variability, fragments were collected as follows: from shaded habitats, only healthy colonies were sampled; from exposed habitats, both healthy-looking and bleached colonies were sampled. For each condition (shaded healthy, exposed healthy, exposed bleached), three fragments of approximately 2 cm were collected from each of three parent colonies (n=3 per treatment, for each habitat) to assess Φ_{PSII}, $rETR_{max}$, and NPQ_{max}. Coral fragments were collected by snorkeling using pliers and immediately transferred into a bucket of aerated seawater for transport. Samples were then brought to the laboratory for subsequent experimental trials.

Ex situ thermal stress experiment

For the thermal stress experiment, only healthy-looking *E. forskaliana* fragments were selected from the exposed habitat to ensure uniform health conditions and minimize initial stress, maintaining experimental consistency. Fragments of *E. forskaliana* collected from shaded and exposed reef habitats were placed in separate closed aerated tanks (80 × 60 × 42.5 cm) filled with natural seawater. Coral fragments were acclimated at 29°C for 48 hours prior to the experiment. Water movement was maintained using circulation pumps, and temperature was regulated using thermostats. Salinity was monitored at regular intervals with a refractometer, and any slight increases were adjusted by gradually adding small volumes of distilled water.

These tanks corresponded to two distinct temperature treatments: 29°C, representing natural ambient conditions, and 32°C, simulating elevated thermal stress typical of bleaching events. The temperature was gradually increased at a rate of 1°C per hour until reaching 32°C. For each temperature regime, three fragments from shaded and exposed habitats were included. Temperature and light intensity were recorded at 15-minute intervals using HOBO Pendant® Temperature/Light sensors. Light intensity measurements recorded in lux were converted to photosynthetically active radiation (PAR) in µmol photons m^{-2} s^{-1} using a standard calibration factor of 0.0135, corresponding to cool white fluorescent lamps. To assess the photosynthetic performance and stress responses of the in hospite symbiont, effective quantum yield (Φ_{PSII}), relative electron transport rate ($rETR_{max}$), and non-photochemical quenching (NPQ_{max}) measurements were recorded at three time intervals to monitor the effects of thermal stress over time: before temperature exposure, after 3h, and 12 h to observe the short-term effects of thermal stress to capture the early stress signatures before the onset of visible bleaching (Bhagooli and Hidaka 2003).

Data analysis

The assumption of normality for each group (shaded and exposed conditions) was evaluated using the Shapiro-Wilk test. To assess differences in the mean diameter of coral colonies between shaded and exposed conditions, an independent t-test was conducted. The experimental data for effective quantum yield, relative electron transport rate ($rETR_{max}$), and non-photochemical quenching (NPQ_{max}) in 2018 were arcsine (square-root) transformed before Analysis of Variance (ANOVA) to ensure normality. An independent t-test was performed to compare means of effective quantum yield (Φ_{PSII}), relative electron transport rate ($rETR_{max}$), and non-photochemical quenching (NPQ_{max}) for the *in hospite* symbiont between shaded and exposed conditions. All statistical analyses were performed using IBM SPSS 21.

RESULTS AND DISCUSSION

In situ temperature variation in exposed and shaded habitats

Temperature in the exposed habitat ranged from 26.7°C to a maximum of 33.0°C, with a daily fluctuation of up to 5.2°C, and the area experienced a more pronounced temperature increase during daylight hours, peaking around midday. The shaded habitat exhibited a lower and less variable temperature range of about 2.5°C, fluctuating between 26.2°C and a maximum of 30.3°C (Figure 3.A). These temperature data were recorded continuously over two days, capturing diurnal thermal variability in both habitats.

Light intensity in the exposed habitat reached a maximum of around 203.9 µmol m^{-2} s^{-1} (11022 lux), showing significant fluctuations throughout the day and a sharp peak pattern during midday. The shaded habitat maintained a much lower light intensity of approximately a maximum of 6.99 µmol m^{-2} s^{-1} (378 lux) (Figure 3.B).

Pre-existing differences in colony morphometrics and pigmentation across reef zones

During initial field observations, noticeable differences in coral morphology and pigmentation were noted across reef zones. Colonies situated in shaded environments were typically larger and more pigmented, whereas those in exposed areas appeared smaller and paler. These characteristics were evident before any thermal stress was applied, suggesting they are characteristic of each habitat rather than signs of bleaching. These site-specific baseline differences were carefully accounted for throughout the study to ensure that natural variability was not misinterpreted as bleaching.

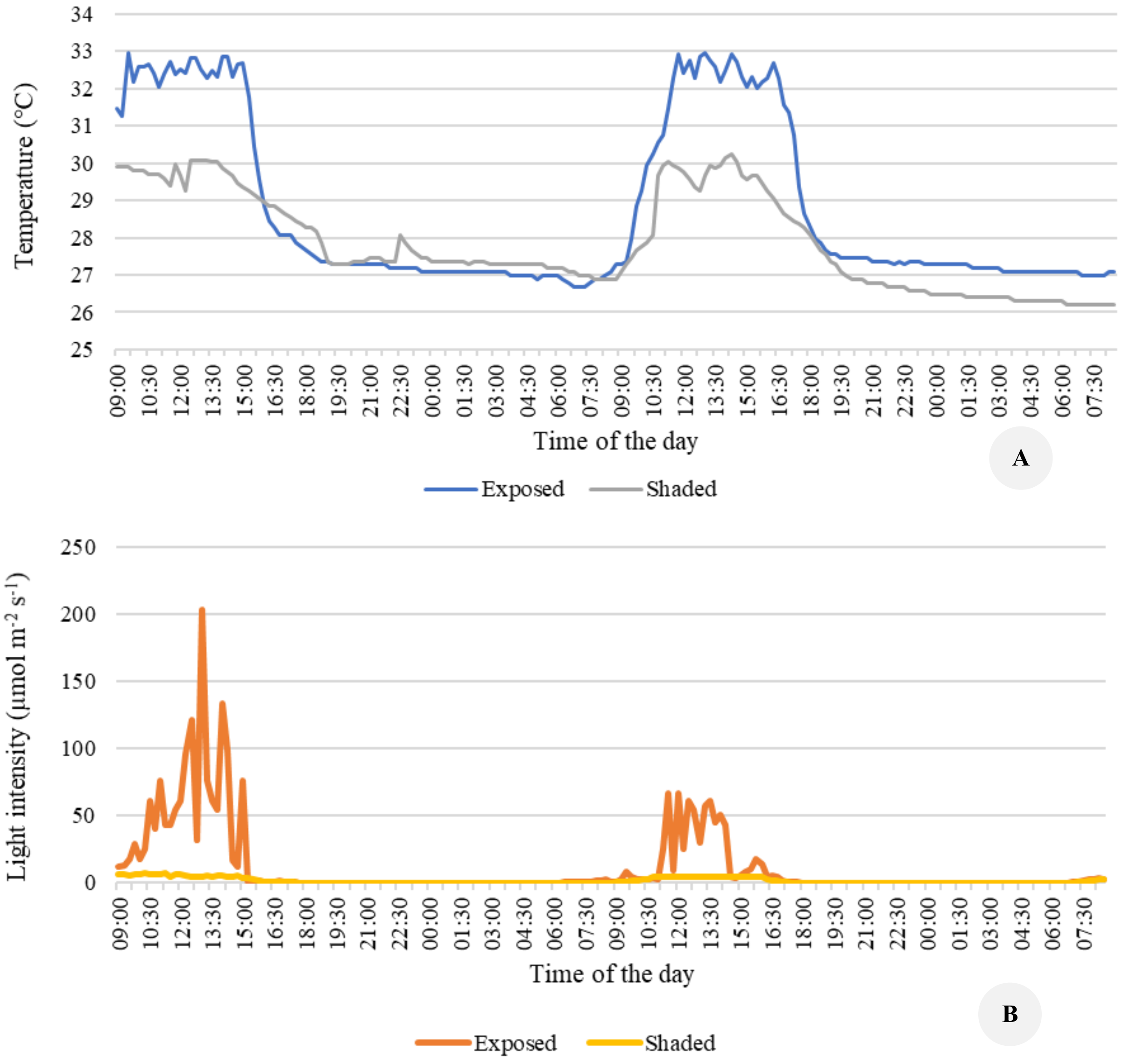

Figure 3. A. Temperature (°C); and B. light intensity (µmol m^{-2} s^{-1}) recorded from data loggers in shaded and exposed conditions at St. François, Rodrigues Island, recorded in April 2018

Bleaching and coral size survey

The bleaching survey revealed a higher percentage of pale/bleached colonies in exposed environments compared to the shaded ones (Figure 4.A). In exposed conditions, 93.3±5.8 % of the colonies displayed bleaching conditions, while no bleaching was observed in shaded colonies. Colony diameter measurements (Figure 4.B) highlighted that there was a significant difference ($p<0.05$, independent t-test) in mean colony diameter between shaded and exposed environments. Colonies in shaded environments had larger average diameters (42.±9.0 cm) compared to those in exposed environments, which were smaller (12.6±3.4 cm). Visual observations indicated a color difference between healthy-looking shaded and exposed colonies, with shaded ones appearing more pigmented than their exposed counterparts (Figure 2).

Thermal photo-physiological response of *E. forskaliana* under experimental conditions

The temperature-controlled tanks successfully maintained distinct thermal conditions, with an average temperature of 29.0±0.26°C in the 29°C treatment and 32.0±0.04°C in the 32°C treatment (Figure 5.A). While temperature remained stable within each treatment, light levels showed minor fluctuations throughout the experiment. The average light intensity in the 32°C tanks was 2.79±0.36 µmol m^{-2} s^{-1} (206.5±27.0 lux), while the 29°C tanks had a similar average light intensity of 2.80±0.030 µmol m^{-2} s^{-1} (207.7±21.9 lux) (Figure 5.B).

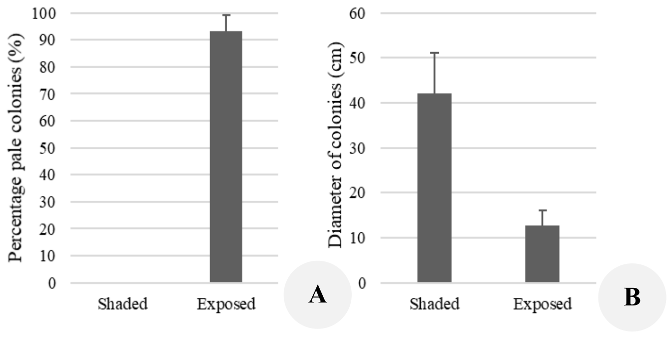

Figure 4. A. Percentage pale (bleached) colonies; and B. Diameter of colonies (out of 10 colonies for *E. forskaliana*) in shaded and exposed habitats at St. François, Rodrigues Island, recorded in 2018. Bars represent mean ± SD (n=10)

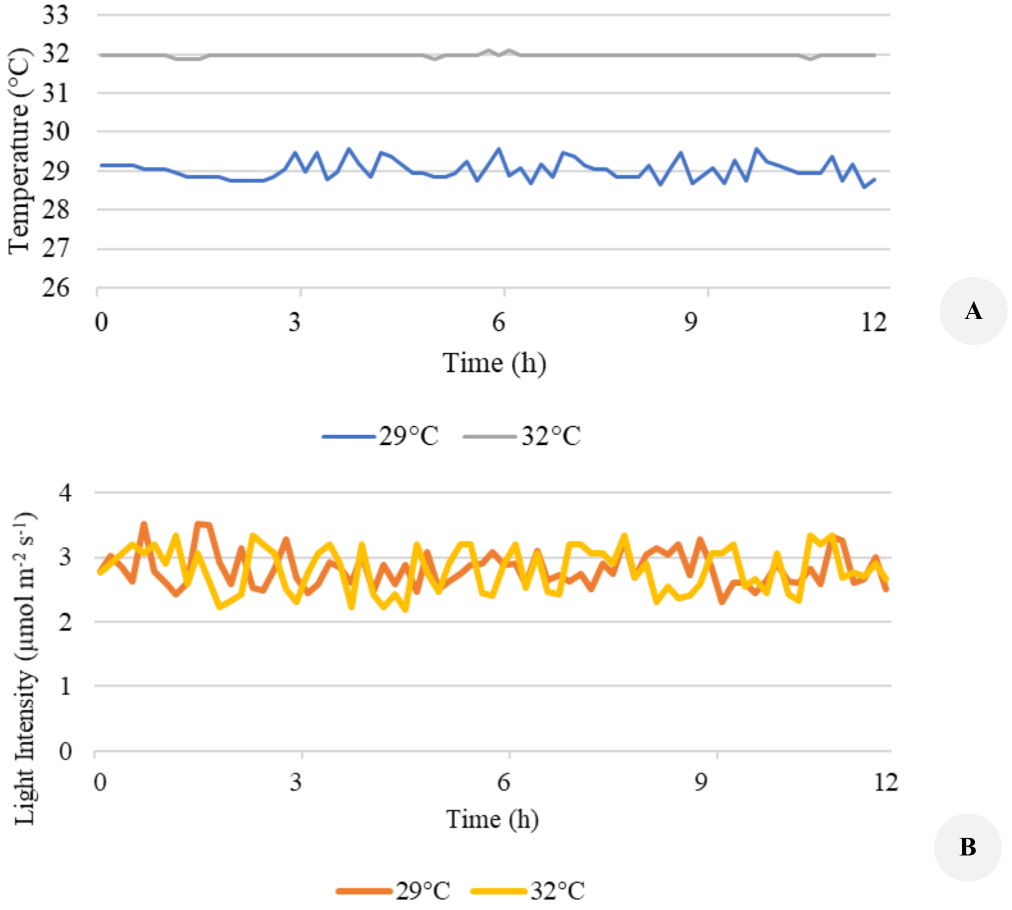

Figure 5. A. Temperature (°C); and B. light intensity (µmol m^{-2} s^{-1}) recorded from data loggers set in the experimental tanks exposed to different temperatures (29 and 32°C) and light exposures

Thermal photo-physiological responses of healthy-looking and bleached *E. forskaliana* from shaded and exposed habitats

Field-based photo-physiological assessments indicated slight but consistent differences in the responses of *E. forskaliana* colonies inhabiting shaded and exposed environments. Shaded colonies exhibited slightly higher Φ_{PSII} compared to exposed colonies in a healthy-looking state; however, no significant difference was noted (t-test, $p>0.05$). Bleached colonies, however, showed a decrease in Φ_{PSII} compared to healthy colonies, in the exposed site (Figure 6.A). The maximum relative electron transport rate ($rETR_{max}$) did not vary significantly (t-test, $p>0.05$) between shaded and exposed colonies for either healthy-looking or bleached conditions (Figure 6.B). Nonetheless, bleached colonies displayed a slight reduction in $rETR_{max}$. Non-photochemical quenching (NPQ_{max}) was significantly higher (t-test, $p<0.05$) in healthy-looking exposed colonies compared to their shaded counterparts. Conversely, exposed bleached colonies showed markedly higher NPQ_{max} than the healthy-looking shaded colonies (Figure 6.C). The healthy-looking and bleached colonies in the exposed conditions exhibited similar NPQ_{max} (0.563±0.107).

There was a significant difference ($p<0.05$) in Φ_{PSII}, $rETR_{max}$, and NPQ_{max} between shaded and exposed habitats. Additionally, a significant difference ($p<0.05$) was found in Φ_{PSII} and NPQ_{max} due to the combined effects of shaded/exposed conditions, time of exposure, and temperature (Table 1). The Φ_{PSII} for the shaded colonies remained relatively stable across all conditions. However, the exposed colonies exhibited a significant decline at 32°C after 12 hours of exposure from 0.601 to 0.0013, representing a 99.7% reduction in Φ_{PSII} (Figure 7.A).

The shaded *E. forskaliana* colonies consistently maintained higher $rETR_{max}$ values across all conditions compared to the exposed colonies (Figure 7.B). Both shaded and exposed colonies exhibited a decline in $rETR_{max}$ at 32°C compared to initial ($p<0.05$) and 29°C conditions (shaded: $p<0.05$; exposed: $p<0.05$), with the ones from exposed conditions having even lower $rETR_{max}$ than the shaded ones ($p<0.05$). At 29°C, shaded colonies exhibited a 4.0% decrease in $rETR_{max}$ from initial values (55.9±3.4) to 3 h (53.7±4.8) and a further 2.3% decrease after 12 h (to 52.4±5.7) (significant over time, $p<0.05$). In contrast, exposed colonies experienced a larger reduction, with a 9.6% decline in $rETR_{max}$ from initial values (46.8±11.6) to 3 h (42.3±9.5) and a 5.8% decrease after 12 h (to 44.0±13.0) (not significant over time: $p>0.05$). At 32°C, shaded colonies experienced a dramatic 87.1% decline in $rETR_{max}$ after 3 h (from 55.9±3.4 to 7.2±1.4) and a 96.9% decline after 12 h (from 55.9±3.4 to 1.8±0.5) ($p<0.05$). Exposed colonies showed an even more severe decline ($p<0.05$), with a 91.4% reduction after 3 h (from 46.8±11.6 to 4.0±1.2) and a complete collapse after 12 h (from 46.8±11.6 to 0.5±0.4).

In the shaded colonies, NPQ_{max} increased moderately over time, although these changes were not statistically significant ($p>0.05$). However, in the exposed samples, NPQ_{max} were higher initially and in the 29°C treatment, though differences were not significant ($p>0.05$). In 32°C treatment, the shaded colonies had a higher NPQ_{max} compared to colonies from exposed habitats, both after 3h ($p<0.05$) and 12 h ($p<0.05$ treatments (Figure 7.C). In shaded colonies, the NPQ_{max} decreased by 38.29%, while in exposed conditions, a 97.37% decline was observed from 3h to 12 h treatment ($p<0.05$).

Discussion

With the increasing global frequency and duration of marine heatwaves, the intensity and occurrence of coral bleaching are expected to rise. However, even during extreme warming events, bleaching patterns can vary considerably across different areas of the reefscape, influenced by local environmental factors such as light exposure, water flow, and depth (Grottoli et al. 2017; Schoepf et al. 2020; van Woesik et al. 2022). The results of this study show how environmental conditions greatly impact the photo-physiological performance and thermal stress responses of *E. forskaliana* colonies from shaded and exposed habitats.

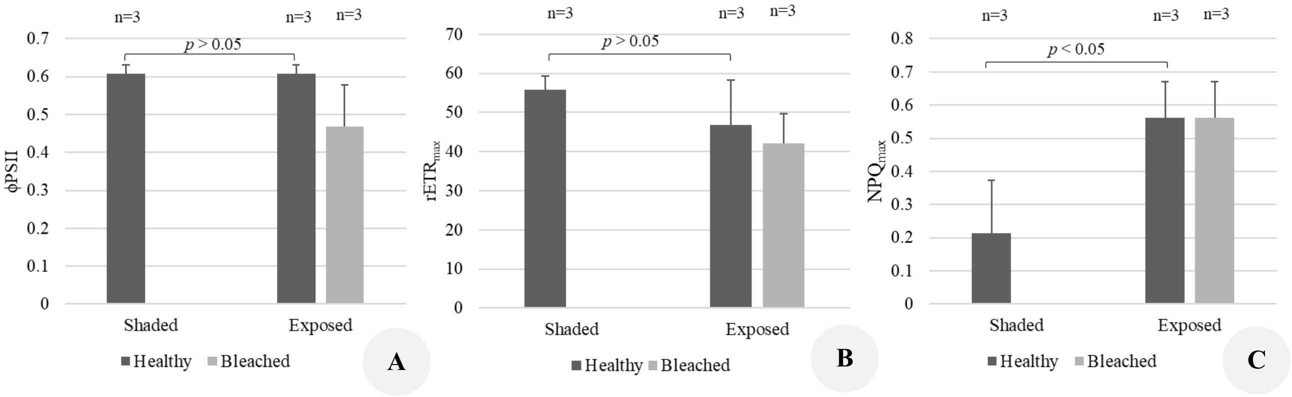

Figure 6. A. Effective quantum yield (Φ_{PSII}); B. Maximum relative electron transport rate ($rETR_{max}$); C. Non-photochemical quenching (NPQ_{max}) for in hospite zooxanthellae of the shaded and exposed colonies of healthy-looking and bleached *E. forskaliana.* Bars represent mean ± SD (n=3). Sample sizes (n) are indicated for each condition. Note that no bleached colonies were observed at the shaded site. Different letters above bars indicate statistically significant differences (t-test, $p<0.05$)

Table 1. Summary of three-way ANOVA on effects of conditions (shaded vs exposed), time of exposure, and temperature on the effective quantum yield (ΦPSII), relative maximum electron transport (rETRmax), and non-photochemical quenching (NPQ$_{max}$) *in hospite* zooxanthellae of *E. forskaliana*. Asterisks represent significant differences at P<0.05 *, P<0.01 **, P<0.001 ***, and NS indicates no significant difference

Photo- physiological parameters		**ϕPSII**			**rETR$_{max}$**			**NPQ$_{max}$**		
Source of variation	**ANOVA**									
	DF	**MS**	***F***	***P***	**MS**	***F***	***P***	**MS**	***F***	***P***
Conditions	1	0.001	125.948	0.000***	0.076	13.714	0.001**	0.002	14.876	0.000***
Time of exposure	2	0.003	446.938	0.000***	0.467	83.736	0.000***	0.108	1061.533	0.000***
Temperature	1	0.002	394.637	0.000***	1.467	263.119	0.000***	0.000	1.762	0.197^{NS}
Shaded and exposed conditions × Time	2	0.001	123.971	0.000***	0.000	0.002	0.998^{NS}	0.000	4.404	0.023*
Shaded and exposed conditions × Temperature	1	0.001	115.807	0.000***	0.000	0.060	0.809^{NS}	0.002	21.203	0.000***
Time × Temperature	2	0.002	418.273	0.000***	0.384	68.908	0.000***	0.002	16.087	0.000***
Shaded and exposed conditions × time × Temperature	2	0.001	120.978	0.000***	0.001	0.107	0.899^{NS}	0.005	51.670	0.000***

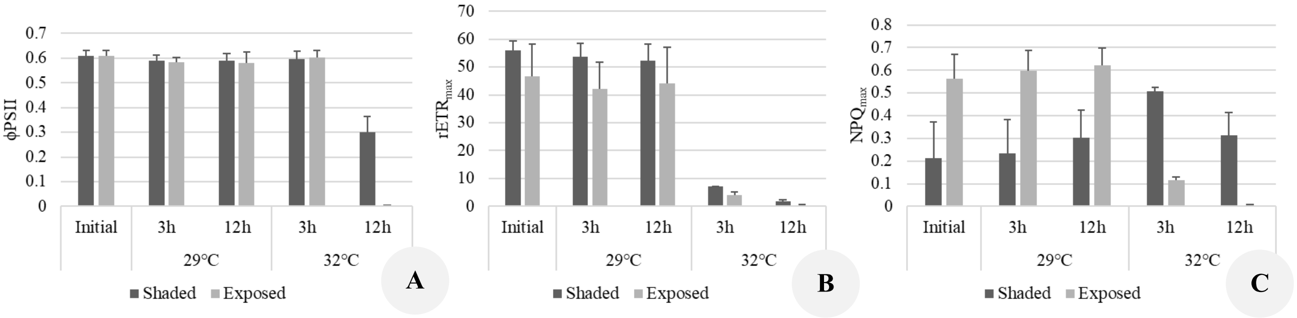

Figure 7. A. Effective quantum yield (Φ$_{PSII}$); B. Relative maximum electron transport rate (rETR$_{max}$); C. Non-photochemical quenching (NPQ$_{max}$) initially, after 3h and 12h exposure at 29 and 32°C stress exposure for *in hospite* zooxanthellae of the shaded and exposed *E. forskaliana*. Bars represent mean ± SD (n=3)

In addition to heat stress, the extent of coral bleaching is also influenced by light intensity. Therefore, providing shade to corals by blocking direct sunlight can help lessen the bleaching impact caused by higher ocean temperatures (Hoegh-Guldberg 1999; Swain et al. 2016). Bleaching surveys revealed a significant disparity between the two environments, with 93.3% of colonies in exposed habitats showing signs of bleaching, while shaded areas remained unaffected. The findings of the survey support the findings of previous studies (Baker et al. 2008; Hoogenboom et al. 2017; Muir et al. 2017; Van Woesik and McCaffrey 2017), which suggested that corals in shaded areas are less susceptible to bleaching when exposed to high-temperature stress, unlike their counterparts in more exposed environments. Conversely, some studies highlight potential drawbacks of reduced light availability, such as increased turbidity negatively affecting coral health (Fisher et al. 2019; Juhi et al. 2021; López-Londoño et al. 2021). Furthermore, experimental evidence has shown that thermal bleaching can still occur in the absence of light and photosynthesis, suggesting additional, yet unidentified, bleaching mechanisms (Tolleter et al. 2013).

Light significantly impacts coral calcification and metabolism by enhancing photosynthesis in algal symbionts, which supports coral growth (Mallon et al. 2022; Neder et al. 2022; Ross et al. 2022; Izumi et al. 2023). This aligns with the observed differences in *E. forskaliana* colonies at St. François, where those in exposed environments, receiving higher light intensities, were smaller and less pigmented compared to the larger, more pigmented colonies found in shaded areas. Similar studies have shown that artificial shading positively influences coral growth and pigmentation, with non-shaded corals exhibiting slower growth and reduced coloration (Coelho et al. 2017). Smaller colonies in exposed habitats likely reflect limited growth due to environmental stressors such as high light intensity and temperature fluctuations (Fabricius 2006). Additionally, coral colony geometry influences light availability, photoacclimation, and energy balance, shaping the light niche of symbiotic corals (Enríquez et al. 2017; López-Londoño et al. 2024). Other studies have shown that coral polyps exposed to less direct sunlight display lower levels of bleaching. This effect was especially evident in polyps located on parts of the colony that faced away from the main angle of solar exposure or were protected within crevices and fissures (Glynn and D'Croz 1990). In contrast, shaded habitats seem to reduce thermal stress, emphasizing their importance as crucial refuges for more resilient coral populations (Baker et al. 2008). Evidence from experimental and field studies indicates that certain coral taxa maintain photosynthetic performance and growth under reduced light, and that shading responses are highly species-dependent (Rosic et al. 2020; Ellis et al. 2024). Consequently, coral responses to shading cannot be generalized and must be interpreted in the context of species-specific physiological traits and adaptive capacities.

This study observed differences in photo-physiological responses and pigmentation between corals from different light environments, suggesting habitat-linked physiological adaptations. Recent studies have also highlighted species-specific resilience patterns, emphasizing the role of local adaptation and physiological plasticity in modulating thermal stress responses (Morais et al. 2024). One possible explanation for the observed variation is the presence of different symbiont types across habitats. While symbiont genotyping was not performed in this study, previous research suggested that such photo-physiological variability could stem from differences in symbiont types within the same coral species. A study by Bhagooli (2009) revealed that *Stylophora pistillata* (Esper, 1792) (susceptible) and *Platygyra ryukyuensis* Yabe & Sugiyama, 1935 (resistant) corals, when exposed to elevated temperatures, exhibited distinct photo-physiological responses in their symbiont, with differing ITS2 genotypes showing variations in heat dissipation and electron transport rates, potentially explaining their differential susceptibility to bleaching. Tilstra et al. (2017) also highlighted the variability in physiological responses within individual *S. pistillata* corals, suggesting that differences among the spatially distinct clades of this species may contribute to this variability. Similarly, research by Winters et al. (2009) found that the composition of zooxanthellae in *S. pistillata* varies with light exposure. Deeper colonies were associated with *Cladocopium* species (clade C), while shallower colonies hosted *Symbiodinium* species (clade A), influencing their ability to tolerate thermal stress. *Symbiodinium* species (Clade A) has demonstrated the ability to dissociate antenna complexes from PSII under high light, enhancing host survival and bleaching resistance. As the most ancestral type, it has retained key protective mechanisms, which help minimize PSII damage, enhance NPQ through xanthophyll de-epoxidation, and facilitate UV protection via UV-protective mycosporine-like amino acids (MAAs) production, unlike deeper-dwelling corals with non-Clade A symbionts (Reynolds et al. 2008; Fujise et al. 2018). Similarly, darker pigmentation in corals from low-light environments may reflect higher chlorophyll concentrations, a trait associated with increased light-harvesting capacity but potentially greater vulnerability under thermal stress. These patterns align with studies that report species- and habitat-specific plasticity in coral thermal tolerance (Kenkel et al. 2015; Mizerek et al. 2018; Kuanui et al. 2020; Dobson et al. 2021; Morais et al. 2024; Ellis et al. 2024). These findings suggest that coral symbiont composition and pigmentation adjust in response to changes in light intensity, which significantly affects coral health and their ability to withstand environmental stressors. Understanding these adaptive responses is vital for predicting how corals will cope with climate change and for creating targeted conservation strategies.

The observed differences in Φ_{PSII}, $rETR_{max}$, and NPQ_{max} between shaded and exposed *E. forskaliana* colonies can be attributed to variations in light exposure and thermal stress tolerance. The significant decline in Φ_{PSII} in exposed colonies at 32°C suggests severe photoinhibition and damage to the photosynthetic apparatus, likely due to excessive light stress and impaired repair mechanisms (Lesser 2021). This aligns with the findings of Jones et al. (1998), which suggested that heat stress in *S. pistillata* initially impacts the Calvin cycle, with photoinhibition of PSII as a secondary effect, exacerbated by light. It is noteworthy that Bhagooli (2013) showed that in *S. pistillata*, bleaching occurred due to interruption of the Calvin-Benson cycle, associated with increased photoinhibition through suppression of repair of the protein synthesis at PSII. Further research by Bhagooli and Hidaka (2003, 2004) demonstrated that thermal stress reduces the light intensity threshold for photoinhibition differently in these coral species, leading to increased bleaching and mortality in *S. pistillata*, but no mortality in *P. ryukyuensis*, with zooxanthellae from different corals showing varying stress tolerances. In contrast, shaded colonies maintained more stable Φ_{PSII}, indicating better photoprotection and sustained photosynthetic efficiency. Similarly, the greater decline in $rETR_{max}$ in exposed colonies compared to shaded ones highlights their reduced ability to maintain electron transport under high temperatures, potentially due to increased oxidative stress and damage to Photosystem II (Yakovleva and Hidaka 2004). The contrasting NPQ_{max} responses further support this explanation; shaded colonies exhibited a more controlled increase in NPQ_{max} at 32°C, suggesting an adaptive photoprotective response to dissipate excess energy, whereas exposed colonies showed a sharp decline, indicating a breakdown in their capacity for non-photochemical quenching. The inability of exposed colonies to regulate excess energy dissipation likely exacerbated photodamage, ultimately leading to higher susceptibility to bleaching.

This study highlights the significance of microhabitats as natural refuges against climate stress, offering corals in shaded or structurally intricate reef environments a buffer from extreme heat and light exposure. These protective areas, including mesophotic reefs, deeper slopes, and overhangs, are associated with higher coral survival during major bleaching episodes. However, recovery in turbid environments can be slower due to recurring disturbances (Evans et al. 2020). Light naturally diminishes with depth (Kahng et al. 2019), while temperature variations are less predictable (Bongaerts et al. 2010). In some instances, deeper reef areas experience lower temperatures (Prasetia et al. 2016), which may contribute to reduced bleaching and mortality rates at greater depths (Glynn 1996). During the 2016 bleaching of the northern Great Barrier Reef, coral bleaching prevalence declined with depth, likely due to reduced light exposure (Baird et al. 2018; Frade et al. 2018). However, it's important to note that species-specific variability indicates that depth-mediated thermal refugia are not universally effective. This variability should caution us against generalizing the protective effects of microhabitats. Overall, these findings highlight the protective role of shaded habitats in mitigating light and thermal stress on corals. By understanding the mechanisms underlying coral resilience, conservation efforts can prioritize the preservation of these microhabitats to enhance reef survival in an era of climate change.

In conclusion, this study highlights the significant impact of habitat conditions, exposure duration, and temperature on the photo-physiological performance and thermal stress responses of *Echinopora forskaliana* colonies in both shaded and exposed environments. The results emphasize the protective advantages of shaded habitats, where corals showed increased resilience to bleaching and thermal stress experiments. Shaded colonies showed larger sizes, more stable photo-physiological metrics (Φ_{PSII}, $rETR_{max}$, and NPQ_{max}), and higher thermal tolerance compared to exposed colonies. Conversely, exposed colonies experienced notable declines in these metrics, especially at higher temperatures, indicating their greater vulnerability to thermal stress and bleaching. These results underscore the importance of habitat structure in coral health, with shaded areas offering a potential refuge for corals amid climate change-driven ocean warming. Focusing conservation efforts on these shaded microhabitats could enhance coral resilience, which may be vital for the long-term survival of coral reefs as sea temperatures continue to rise.

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Aggregation behavior of suspension-feeding sea cucumbers in a tropical lagoon system of Rodrigues Island, Western Indian Ocean

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Abstract. *Gerzer F, Kaullysing D, Ramah S, Bhagooli R. 2025. Aggregation behavior of suspension-feeding sea cucumbers in a tropical lagoon system of Rodrigues Island, Western Indian Ocean. Indo Pac J Ocean Life 9: 124-132.* Suspension-feeding holothurians exhibit unique behavioral and ecological adaptations when compared to deposit-feeding sea cucumbers. Their population drivers, habitat preferences, and niche partitioning, however, remain poorly understood. In this study, we document a high-density aggregation of *Holothuria cinerascens* (Brandt, 1835) (16.9 ± 3.11 ind/m²), which was substantially higher than the coexisting deposit-feeders' density (*Holothuria atra* Jaeger, 1833: 0.8 ± 0.9 ind/m²; *Stichopus horrens* Selenka, 1867: 0.3 ± 0.5 ind/m²). The study site in Torrent, located on Rodrigues Island's east coast, is characterized by sandy flats and occasional limestone structures that clearly indicate habitat partitioning. The limestone structure along the transect showed 100% niche occupation by *H. cinerascens*, and the sandy flat had a composition of 72.7% *H. atra* and 27.3% *S. horrens*. The limestone's structural complexity provides a variety of crevices, access to water flow, predatory refuge, and attachment opportunities, ultimately creating a suitable habitat for suspension-feeding holothurians. Additionally, trade wind-generated hydrodynamics on Rodrigues Island likely enhance suspended nutrient flux on the east coast, favoring suspension-feeding plasticity of the sometimes trophically facultative *H. cinerascens*. These findings give insights into holothurian niche specialization, driven by microhabitat structure, hydrodynamic conditions, and trophic plasticity, delivering possible implications on conservation and mariculture strategies, as well as enhancing the overall understanding of holothurian ecology.

Keywords: Biogeograph aggregation behavior, high density occurrence, *Holothuria cinerascens*, niche differentiation, suspension-feeding sea cucumber

Abbreviations: H': Shannon diversity index, J': Pielou's evenness, S: Species richness

INTRODUCTION

Sea cucumbers are a diverse group of mostly benthic marine echinoderms with a variety of ecological functions. Their active behavior of digging and burrowing through benthic habitats makes them a significant contributor to marine bioturbation and sediment redistribution. Their feeding behavior of either deposit-feeding or suspension-feeding reduces the organic load, while the excretion of inorganic phosphorus and nitrogen enhances benthic biota productivity. Their ecological capability of symbiotic relationships enables them to host around 200 commensal and parasitic symbionts, significantly boosting marine biodiversity, as well as, being prey for trophically higher taxa displays their role in transferring detritus- and macroalgae-derived nutrients along the food web, which does not only highlight their ecological importance in maintaining ecosystem functioning and connecting benthic communities to the nekton but also their potential use for bioremediation (Purcell et al. 2016; Ribani et al. 2024).

In addition, sea cucumbers regenerate nutrients in coral reefs, alter carbonate content and pH of the surrounding water (Sun et al. 2018), enhance ammonium concentration through respiratory expulsion (Uthicke 2001), increase mineralization in organically-enriched sediments (Pierrat et al. 2021), control the growth of the microphytobenthos through grazing, decompose organic matter, and cause sediment-seawater exchange of dissolved oxygen (Mactavish et al. 2012) and reduce harmful algal blooms through feeding (Mohsen et al. 2020).

Furthermore, sea cucumber declines have been linked to increases in coral disease susceptibility, as they can reduce the pathogen load of the sediment and make the sediment microbiome less suitable for pathogens to thrive (Grayson et al. 2022; Clements et al. 2024). While deposit-feeding holothurians ingest sediment material that has been deposited on the benthos, suspension-feeding holothurians use their oral tentacles to filter particles suspended in the water column (Pierrat et al. 2021; Kabanova and Filgueira 2024). Most deposit-feeding holothurians are epibenthic deposit-feeders, meaning their feeding habitat is on the surface of sediments (Pierrat et al. 2021). The diet of deposit-feeders mainly consists of inorganic compounds, micro-organisms, organic matter, and fecal pellets (Dar and Ahmad 2006). While most sea cucumbers among the *Holothuria* (Linnaeus 1767) genus are deposit-feeders, *Holothuria cinerascens* (Brandt, 1835), which will be discussed in this study, stands out as a suspension-feeder (Purcell et al. 2016; Ahmed et al. 2023) with a diet consisting mainly of plankton, detritus, and other micro-organisms in the water column (Ahmed et al. 2021).

A variety of different factors influence the behavior of sea cucumbers. Changes in salinity, for instance, have shown effects on the feeding and burrowing cycles of sea cucumbers, causing some species to burrow themselves in the sediments during periods of decreased salinity (Mercier et al. 2000; Domínguez-Godino and González-Wangüemert 2020). Temperature and different thermal regimes also have an impact on the burrowing behavior of sea cucumbers (Zhang and Lai 2024). On Palawan Island in the Philippines, water flow and current variations have been shown to affect sea cucumber distribution and activity directly (Jontila 2017).

During reproductive periods, sea cucumbers have been observed to exhibit aggregation behavior (Mercier et al. 2000). Male individuals can release olfactory chemicals, attracting both females and males to initiate reproduction and spawning (Marquet et al. 2018). While some sea cucumbers have developed predatory-defense mechanisms, such as the excretion of Cuvierian tubules, evisceration, or possess toxins that make them undesirable prey (Conand 2008), others prefer to use their soft bodies to engulf themselves in small crevices.

There is an increasing interest in the potential commercial value of *H. cinerascens* due to its collagen moisturizing properties for cosmeceuticals (Badilli and Inal 2025). In the food industry, holothurians are recognized for their nutritional value, as they are low in fat, sugar, and cholesterol, and rich in minerals, vitamins, collagen, proteins, and polyunsaturated fatty acids (Ghallab et al. 2025). While approximately 90% of the market share of sea cucumbers in the food market is accounted for by dried sea cucumbers, some species like *Apostichopus japonicus* (Selenka, 1867) and *Cucumaria frondosa* (Gunnerus, 1767) are also consumed cooked, pickled, or raw (Harini et al. 2024). In areas like China, Japan, and Korea, sea cucumbers have a long history of traditional medicine or culinary uses; however, given the overexploitation of some species, scientists underscore the need for sustainable practices (Pérez-Lloréns and Mouritsen 2024). Within the Western Indian Ocean region, there is a growing market of wild sea cucumber harvesting in Madagascar (Rothamel et al. 2023).

Altogether, studying suspension-feeding sea cucumbers is of utmost importance for the understanding of their ecological importance in benthic-pelagic coupling, biofiltration, and water quality regulation, as well as their applications and possible commercial values. Despite extensive research on holothurian ecology, the behavior of suspension-feeding holothurians remains poorly understood. This study documents a localized high density of the sea cucumber *H. cinerascens* exhibiting localized aggregation behavior in the unique and dynamic lagoon system of Rodrigues Island.

MATERIALS AND METHODS

The study site is located on the east coast of Rodrigues Island, which belongs to the Republic of Mauritius and lies around 400 km north of the Tropic of Capricorn. It forms part of the Mascarene Islands, among which it stands out due to its different geological age and far-reaching lagoon system. The survey area is called Torrent (19°41'16"S 63°30'13"E) and is found off a small peninsula, within the lagoon, north of East Bay / Baie de l'Est (Figure 1). To the south of the peninsula, there is Fumier Beach, and to the north, Coton Beach.

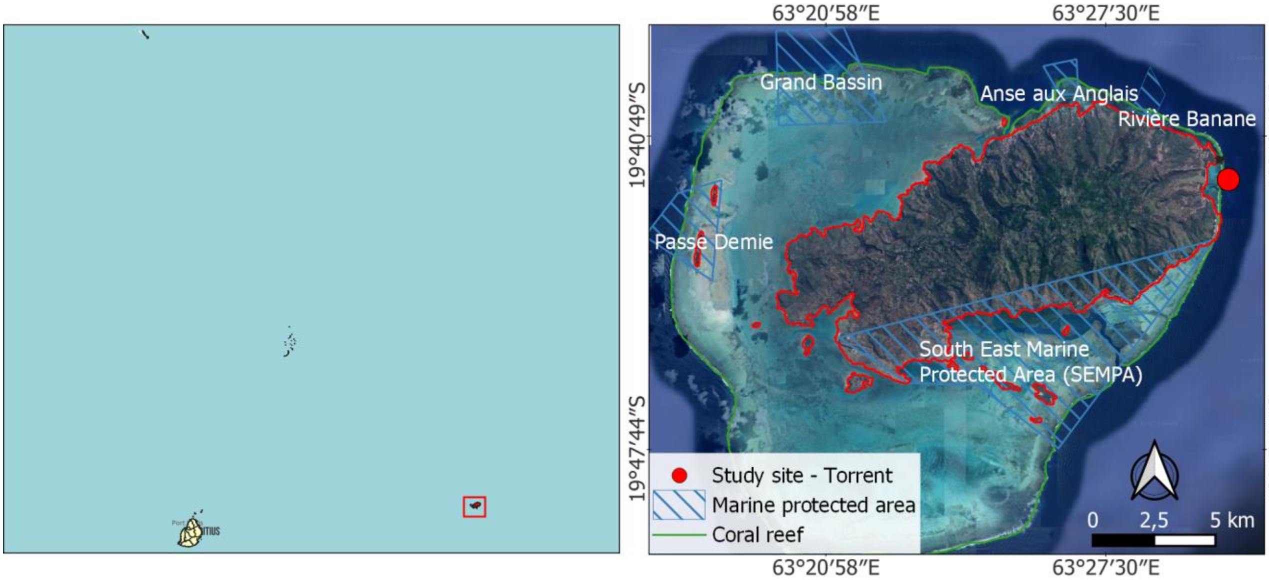

Figure 1. Map of Rodrigues Island showing the location of the survey site of Torrent in Rodrigues Island, Mauritius

A rocky shore with occasional sandy patches characterizes the coastal zone of Torrent. Further inland, behind a small coastal forest, lies a rural area with minimal human development. The lagoon system off Torrent is relatively narrow when compared to the large lagoons of the western part of the Island, and has an approximate depth of 2.6 m. The sea cucumber survey was conducted in April 2017 using ten 1 × 1 m quadrats placed randomly on a large limestone structure and the surrounding sandy benthos at Torrent. Within each quadrat, all sea cucumber species were identified, and their abundance was recorded. Environmental parameters such as habitat type and depth were documented and estimated. Photographs of the sea cucumber species were taken using an Olympus TG4 camera for species identification. Standard lenses and the automatic underwater mode were used for taking the snapshots. Species identification was carried out with the FAO "Commercially Important Sea Cucumbers of the World" guide and the PatriNat "Identification Guide: Commercial Sea Cucumbers" by Marie Di Simone, Arnaud Horellou, Frédéric Ducarme, and Chantal Conand. After the survey, data were compiled to calculate mean densities, which were expressed as individuals of sea cucumber per m^2. Species richness (S), Shannon diversity index (H'), and Pielou's evenness index (J') were calculated using R Studio. Sea cucumber length (in cm) was measured using a handheld wooden ruler. Additionally, visual observations and photographs of substrate type and characteristics were taken along the studied area.

Formula for species richness (S):

$$S = \text{Number of species present in the sample}$$

Formula for Shannon diversity index (H'):

$$H' = -\sum_{i=1}^{S} * \, pi * \, ln \; pi$$

Where: *H'*: Shannon diversity index, *S*: Total number of species in the transect, *pi*: Proportion of individuals of species *i* in the total sample, *ln pi*: Natural logarithm of *pi.*

$$p_i = \frac{\text{Number of individuals of species}}{\text{Total number of individuals in the sample}}$$

Formula for Pielou's evenness index (J'):

$$J' = \frac{H'}{\ln S}$$

Where: J': Pielou's evenness index, H': Shannon diversity index, S: Total number of species in the community (species richness), ln S: The natural logarithm of species richness.

RESULTS AND DISCUSSION

The study site was characterized by a sandy patch with rubble and benthic macroalgae with a depth of around 2.6 m. Within this sandy flat, there was a limestone structure with an approximate length, width, and height of 3.7, 2.3, and 2.2 m, respectively. Additionally, strong currents were observed at the site. Overall species richness is 3, with a value of 1 for the limestone structure and 2 for the sandy flat (Table 1). Shannon's diversity index was 0 on the limestone structure and 0.611 at the sandy flat. Pielou's evenness could not be defined for the limestone structure due to the fact that there was only 1 species present; however, the sandy flat showed an evenness value of 0.881. Sea cucumber density (Figure 2) was higher on the limestone structure than on the surrounding sandy flat, with an average of 16.9 ± 3.1 ind/m² on the limestone structure and 0.55 ± 0.7 ind/m² on the sandy flat. Community composition showed a clear dominance of 100% *H. cinerascens* on the limestone structure, while the sandy flat was composed of 72.7% *Holothuria atra* Jaeger, 1833 (0.8 ± 0.9 ind/m²) and 27.3% of *Stichopus horrens* Selenka, 1867 (0.3 ± 0.5 ind/m²). Sea cucumber species (Figure 3) showed an average length of 18 ± 3 cm for *H. cinerascens*, 7.5 ± 1.6 cm for *H. atra*, and 28 ± 3.6 cm for *S. horrens*.

The results clearly show an unexpected and unusually high-density mass occurrence of *H. cinerascens* (16.9 ± 3.11 ind/m²) on the limestone structure, while the surrounding sandy flat showed relatively low densities (0.55 ± 0.7 ind/m²). While all individuals of *H. cinerascens* recorded at the study site were concentrated on the structure, none were recorded around the sandy flat.

When interpreting these findings, several constraints should be taken into account. This study represents a snapshot documentation of an unusually high-density aggregation of holothurians, while an in-depth analysis of the underlying factors is limited. Hence, the omission of certain variables reduce the ability to draw firm conclusions on the causalities in this aggregation but do decribed and analyze this documented high-denstiy mass aggregation record from the east side of Rodrigues Island that considerably exceeds usual denisties, discusses differences in feeding and habitat derrived habitat requirements of holothurians, and provides an understanding of specific factors influencing aggregation behaviour in holothurians, in order to support a more comprehensive design for subsequent research efforts.

Table 1. Species richness (*S*), Shannon diversity index (*H'*), and Pielou's evenness (*J'*) per habitat type

Habitat type	**Species richness (*S*)**	**Shannon diversity (*H'*)**	**Pielou's evenness (*J'*)**
Limestone structure	1	0	Not defined
Sandy flat	2	0.611	0.881

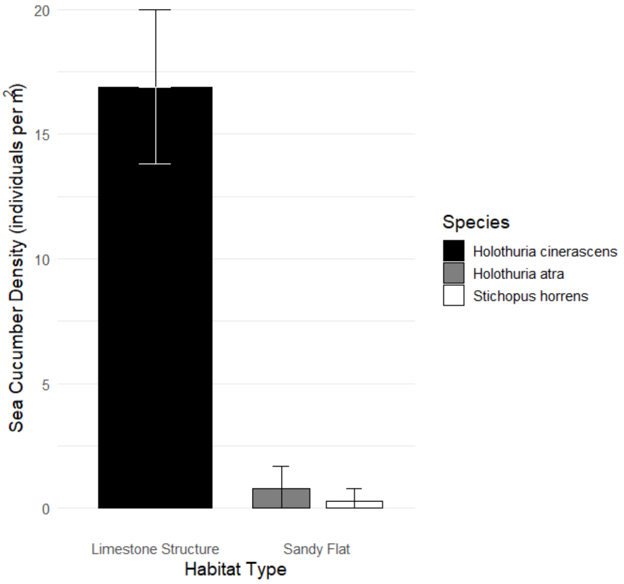

Figure 2. Density of different sea cucumber species by habitat (limestone structure, sandy flat)

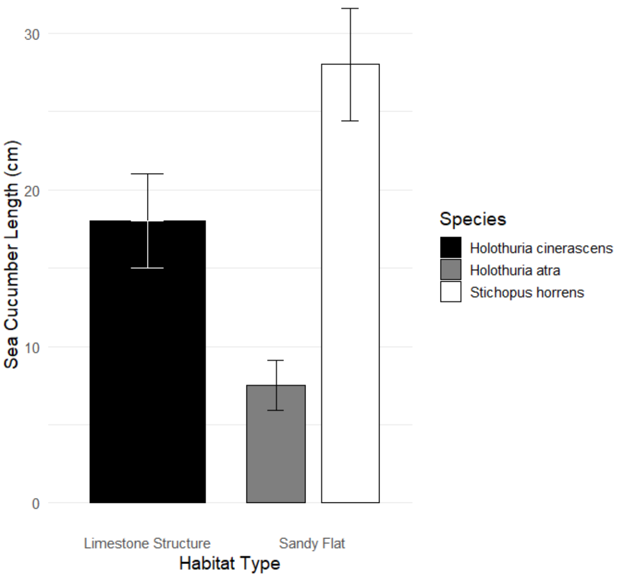

Figure 3. Length of different sea cucumber species (*Holothuria atra, Holothuria cinerascens, Stichopus horrens*)

A study within the Mascarene Island group found a total mean density of sea cucumbers, such as *H. atra* and *Stichopus chloronotus* Brandt, 1835, of 0.59 ± 0.38 ind/m² on sandy flat and coral reef /rubble habitats in La Reunion Island (Conand 2008), aligning with our results concerning deposit-feeding holothurians on the sandy flat substrate. In the Seychelles, a stock survey of two main fishing grounds has revealed an overall standing stock of approximately 0.002 ind/m² (Conand 2008). Throughout the Lakshadweep atolls, an average density of 8 ± 13 ind/m² was found, with numbers ranging from 0 to 177 ind/m². What this example clearly illustrates is that population densities can indeed tend to patchiness, highlighting the importance of understanding aggregation behavior.

The maximum was recorded at the intermediate lagoon area of Chetlat atoll. In the study, *H. atra* (0.37 ± 0.63 to 5.62 ± 24.86 ind/100m²), *S. chloronotus* (0.62 ± 1.11 to 4.76 ± 15.24 individuals/100 m²), and *Actinopyga mauritiana* (Quoy & Gaimard, 1834) (0 to 2.76 ± 3.67 individuals/100 m²) were most common, while *H. cinerascens* (0 to 1.05 ± 1.71 individuals/100 m²) was mainly found along the inner lagoon area, with none observed on the outer reef flat and the reef slope (Mohammednowshad et al. 2021). While Mohammednowshad et al. (2021) describe an east-west difference in species composition to be a major factor in density variations, they also highlight how different habitat zones cause species-specific distribution due to habitat preference. However, in this study, a high-density mass occurrence of non-deposit-feeders has been observed (Figure 4). *Holothuria cinerascens* is one of the few suspension-feeding holothuroids, with most others being deposit-feeders (Purcell et al. 2016). A study by Lampe-Ramdoo et al. (2014) showed an overall density of 0.05 ind/m² of *H. cinerascens* in Mauritius Island with a total of 47 individuals observed over 23 survey sites, posing the question of how such a high density, as observed at Torrent, is possible.

Figure 1 illustrates the crucial role of the lagoon of Torrent, which is notably smaller than the wider lagoons of Rodrigues Island, in influencing sea cucumber distribution. This size difference suggests increased pelagic influences, which are crucial for suspension-feeding sea cucumbers that rely on currents to bring them food. These factors, such as water flow, current strength, current direction, and organic load of food suspended, are the main drivers of density and distribution (Neil et al. 2014; Zhang and Lai 2024). Therefore, areas with strong water flow conditions and high food availability hold greater potential for supporting higher densities of suspension-feeding sea cucumbers. However, the study shows that the strong variation of sea cucumber density in our results is within the same area. This is particularly interesting given the sedentary behavior of suspension-feeding sea cucumbers, which hide in small crevices of reef structures, while holding their tentacles into the current to trap phytoplankton and micro-organisms passing by (Purcell et al. 2016). As explained by Ahmed et al. (2023), *H. cinerascens* relies on a hard substrate that provides a variety of crevices for suitable attachment points in order to extend its large oral tentacles into the current for feeding (Sloan 1979), while also offering protection from predators (Mercier et al. 2000).

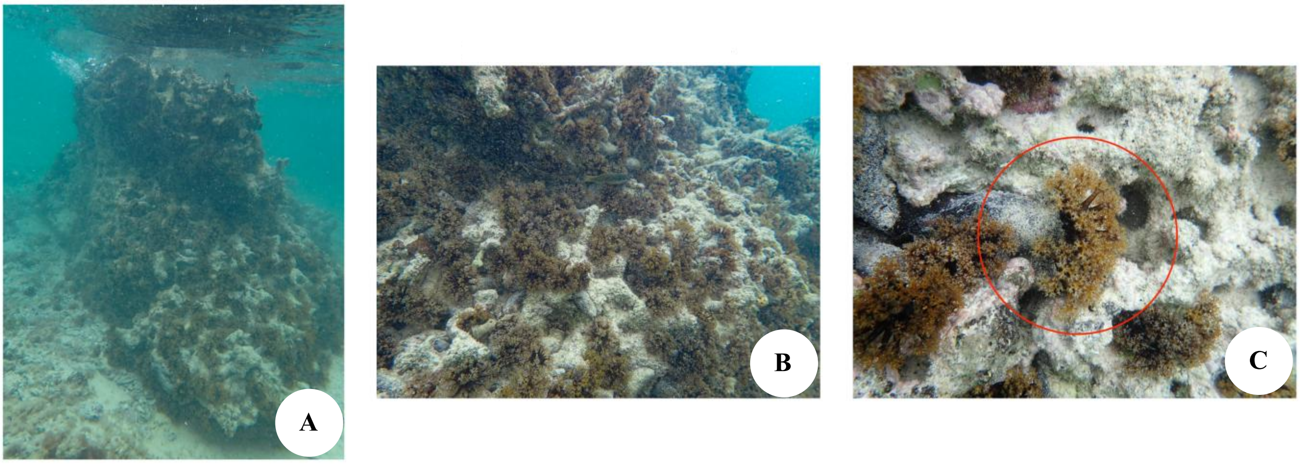

Figure 4. A. Picture of the limestone structure, B. High-density of *Holothuria cinerascens*, C. Oral tentacles protruding from crevices for suspension-feeding

As many holothurian species in Dendrochirotida, Persiculida, Synallactida, and Holothuriida can be opportunistic in their feeding mode, they can shift between suspension- and deposit feeding. Triggers for this shift can be variations in the concentration of suspended particulate organic matter in the water column and changes in water flow velocity, allowing many suspension-feeders to turn to deposited sediments in times of food scarcity or reduced food delivery (Pierrat et al. 2021). While *H. cinerascens* usually carries out suspension-feeding, gut content analysis and ex-situ feeding observations have indicated that *H. cinerascens* can handle deposited nutrients in an opportunistic way, when necessary (Roberts and Bryce 1982; Iwalaye et al. 2020; Ahmed et al. 2023). Hence, observations of behavioural responses to changes in water flow velocity or organic load could be indicative of a possible feeding-induced habitat shift of *H. cinerascens* from the limestone structure towards the sandy flat when nutrient availability in the water column is reduced. Field observations have shown that populations inhabiting the intertidal rocky zone exhibit primarily deposit-feeding behavior. In contrast, populations on outer reefs tend to feed on suspended particles within the water column (Ahmed et al. 2023).

The role of differences in complexity in habitat structure on food resource availability has been shown to ultimately lead to niche partitioning of populations relative to their feeding mechanisms (Pierrat et al. 2021). This is particularly evident in the case of the limestone structure, which was composed of 100% *H. cinerascens*, and the sandy flat, which did not contain a single individual. The direct impact of habitat structure can make higher flow velocity accessible to holothurians (Pan et al. 2015), in particular, can directly affect the distribution of suspension-feeding sea cucumbers (Sebens et al. 2016; Pierrat et al. 2024) is a key finding of this study.

As a result of the southeast trade winds, the Mascarene High, and tropical/extratropical storms from the central and southern Indian Ocean, relative to the geographic location of Mauritius, the east coast of the Island generally experiences higher wave action and increased water flow velocity, both persistent and episodic (Doorga et al. 2018). Due to the similar geographic exposure of Mauritius and Rodrigues Island to these oceanographic conditions, it can be assumed that the east/southeast coast of Rodrigues, as well, experiences increased flow velocity relative to other coasts. Additionally, the fact that the east coast of Rodrigues Island has the narrowest lagoon, compared to the far-stretching lagoons of the north, south, and west (Burney et al. 2015), it is reasonable to assume that the east coast is particularly exposed to high wave energy flux reaching the lagoons from the pelagic, creating strong hydrodynamic conditions (Escudero et al. 2021).

While the low species diversity of the results on the limestone structure precludes inter-specific competition, the possibility of intra-specific competition for food and space, however, could be a major factor in limiting population size, due to the limited niche space available on the habitat structure, ultimately making complexity in habitat structure a main driver for niche specific population biomass (Tanita and Yamada 2019). Variations in water flow, as well as suspended food availability, could be factors that influence the aggregation behavior, feeding cycles, and possible migration patterns of suspension-feeding sea cucumbers, which suggests possible seasonal variations in density and distribution (Hamel and Mercier 1998), hence increasing seasonal interspecific competition for space. As described by Zhang and Lai (2024), high-density aggregations can also be due to reproductive cycles, where male individuals release olfactory biochemicals into the water column to attract both males and females to aggregate at specific locations suitable for reproduction.

Although no reproduction-specific behavior has been observed on the study site, this possible reason that should not be excluded. A study conducted on another Mascarene Island, La Reunion, has taken a novel approach to investigate the reasons why some species of holothurians show patchy distribution patterns. The study, which emphasizes the role of substrate features, habitat type, conspecific attraction, and recruitment aggregations, also highlights the potential impacts of water flow regimes in creating such patchiness (Pierrat et al. 2024). This unique approach has led to significant findings that contribute to our understanding of holothurian distribution patterns. For instance, when comparing deposit-feeding and suspension-feeding holothurians, it becomes clear that suspension-feeding ones typically display a more sedentary behavior, as they do not always need to relocate to obtain food, while deposit-feeding ones must relocate once the sediments around them have been consumed.

An ex-situ experiment by Wang et al. 2023 investigated feeding rate, defecation rate, tentacle activity time, crawling frequency, adhesion time, and righting time of *A. japonicus*. One group was kept in a tank with crevices, and a control group was kept in a tank without crevices. Results have shown that the group with crevices had a significantly higher feeding rate (0.944 ± 0.023) than the control group (0.824 ± 0.026), as well as the defecation rate with 0.132 ± 0.01 and 0.089 ± 0.01, respectively. Potentially indicating a higher feeding efficiency provided by crevices. Tentacle activity time of the crevice group was also higher compared to the control group. Despite crevice-groups indicating more efficient values, crawling frequency did not differ significantly. The study also suggested that crevice availability might help holothurians in managing stressors and supporting overall fitness (Wang et al. 2023). The findings of this study also inspire ex-situ experiments of *H. cinerascens* investigating facultative feeding plasticity when faced with both nutritional resources for suspension- and deposit-feeding. Also, oxygen consumption rates and ammonium excretion rates could be considered to be evaluated when investigating the effects of crevice availability on *H. cinerascens* in ex-situ experiments (Yu et al. 2019). Another study that focused on modelling habitat and substrate preference of holothurians in in-situ surveys concluded that hard substrate typically suggests a higher ability to cope with environmental stressors and sea cucumber length was increasing with total organic matter suspended and decreasing when faced with elevated temperatures (Félix et al. 2024).

Apostichopus japonicus has been found to generally display reduced activity outside of crevices when temperatures rise (Vaschenko and Zhadan 2024), especially concerning early life stages, as rising temperatures have shown to affect larval growth and developmental processes negatively (Lang et al. 2023). An interesting study by Sun et al. (2018) has shown that the suspension-feeding sea cucumber *Cucumaria frondosa* (Gunnerus, 1767) has shown displacement behavior related to water flow and feeding efficiency in areas of weak dynamics by seeking stronger flow exposition for passive suspension-feeding in order to obtain phytoplankton and other suspended particles. Optimal water flow for this species has been shown to be between 21 and 40 cm/s (Sun et al. 2018). At the same time, increased flow velocity has been shown to pose a risk of dislodgement and an increased energy requirement for attachment (Pan et al. 2015).

Some holothurians have been shown to exhibit clumping behavior to enhance resistance to dynamic environments, in order to reduce drag and provide greater surface area for attachment (Brown et al. 2019). Individuals at the survey site (Figure 4) have shown to almost fully embody themselves into the abundant crevices, while protruding the oral tentacles into the current, which does lend strong support to the argument that their nature of aggregation is feeding related. So the limestone structure not only facilitates increased hydrodynamic exposure but also provides a space to engulf themselves in and, thus, reduces drag from increased water flow velocity and gives predation refuge.

The feeding requirements of *H. atra*, on the other hand, are closely related to the organic features of the substrate itself, rather than the positioning provided by the substrate. Enriched sediments with a high load of organic matter, chl-a, and ∂13C have been shown to provide a suitable habitat for holturians like *H. atra* to thrive (Brown et al. 2019). Regarding the habitat requirements for *S. horrens*, studies have shown that individuals do prefer coarser sediments, sand, and rubble habitats (Palomar-Abesamis et al. 2016). These habitat requirements explain the sharp boundary of habitats that causes both the diversity index as well as the evenness (Table 1) to drastically vary over the change of substrate-driven habitat characteristics between the limestone structure and the adjacent sandy flats.

Hence, a size-dependent (Figure 3) habitat selection is doubtful. However, what insight can be obtained from this data is that *H. atra* population seemed to consist mostly of juvenile individuals, as adults range from 12 to 16 cm, with some longer individuals up to 33cm (Pierrat et al. 2024). In a study from the Arabian Sea, adult individuals of *H. cinerascens* measured an average length of 17.8 ± 1.98 cm (Ahmed et al. 2023), which does indicate that individuals documented at the lagoon of Torrent were sexually mature adults. In a study from the Galapagos Islands, individuals of *S. horrens* were found to measure a length of 9-30 cm (Hu et al. 2013), while individuals over 15 cm are generally considered adults (Palomar-Abesamis et al. 2016). This implies that individuals of *S. horrens* documented at the study site are outgrown adults.

Limitations of this study include chemically driven behavior. In a study by Claereboudt et al. (2023), findings show that chemical communication through pheromones can cause holothurians to group. Chemoattraction has been shown to be specifically present when food availability and water quality were high (Pierrat et al. 2024). However, the documented aggregation behavior of this study was not limited to spawning periods.

Subsequent research on high-density mass aggregations of holothurians could benefit from employing a longitudinal design in order to establish causal relationships, such as in-depth habitat analysis of substrate, including dimensions, density, and rougthness of crevices, temporal variability of this aggregation on a both dial and seasonal scale, behavioral analysis of feeding-mechanisms, reproductive behavior, or locomotion documentation, as well as the potential presence of biochemical cues that might trigger aggregation, possible gut analysis and food availability, such as particulate organic matter load or possible small scale chl-a heterogenity to get a deeper insight into diets, and supporting data about environmental conditions as parameters for conclusive evidence on which factors drive such aggregations or could be possible triggers for facultative feeding switches that ultimately causes changes in habitat requirements. Hence, such a more structured design is recommended to investigate underlying mechanisms more thoroughly and provide a more comprehensive understanding of high-density mass aggregations in holothurians. In this specific case of Torrent, subsequent field observations alongside a comprehensive environmental factor influence analysis would shed more light on the temporal variability of this localized aggregation. Frequent monitoring of *H. cinerascens* population at Torrent could be of utmost importance in understanding general aggregation behaviour dynamics of suspension-feeding holothurians.

The deposit-feeding sea cucumber *Holothuria scabra* Jaeger, 1833, for instance, is known to exhibit aggregation behavior linked to specialized metabolites, called saponins, as well as through certain food odors present in the environment (Claereboudt et al. 2023). While generally seen as a sea cucumber with relatively low commercial value, some studies suggest its application for the extraction of collagen for moisturizing cosmetics (Li et al. 2020), as well as possible uses of *H. cinerascens* for aquaculture and bioremediation (Ahmed et al. 2023).

In addition, as described by Džeroski and Drumm (2003), management plans need to take into consideration the broader ecological role of holothurians in ecosystem services, such as food web dynamics, nutrient cycling, water chemistry, and sediment health, highlighting not only the interconnectedness of holothurian dynamics to overall ecosystem functioning but also possible implications of this study in adaptive coastal and ocean management. Studies found that climate change-induced threats, such as rising temperatures, could affect the feeding mechanism of suspension-feeding sea cucumbers by altering tentacle insertion movements (Kabanova and Filgueira 2024).

Thus, in cases of such high-density mass aggregations, coastal managers and marine spatial planners are expected to consider protective measures as ecological impact is not comparable to the usual ecological impact that marine ecosystem uses have on holothurian populations due to an abnormally high abundance of individuals in a specific area that ultimately increases ecological impact on holothurian populations, highlighting the need for context specific assessments. From a pollution-monitoring perspective, holothurians have been shown to be excellent indicators for contamination of microplastics and perfluoroalkyl substances due to their deposit uptake and strong accumulation (Cocci et al. 2025).

The facultative plasticity of *H. cinerascens* suggests a higher adaptive capacity of the species to environmental fluctuations in a changing marine ecosystem. It offers valuable insights into the habitat preferences and behavioral patterns of suspension-feeding sea cucumbers, such as *H. cinerascens*.

By examining the factors driving aggregation and mass occurrences, the findings suggest a non-uniform distribution of these populations influenced by habitat complexity. Such complexity is crucial in promoting niche differentiation in niche-specific communities, ultimately supporting overall reef biodiversity and ecosystem health within complex lagoon systems. Additionally, the results provide useful perspectives for potential aquaculture applications, particularly in multi-trophic systems, by shedding light on how environmental factors determine feeding and aggregation behavior, leading to the possible exploration of *H. cinerascens* implications in aquaculture systems, reducing both suspended particulate organic matter from the water column, as well as deposited organic matter in the sediments.

The results also contribute to improving monitoring strategies for holothurian biodiversity. Suspension-feeding sea cucumbers do not solely rely on strong currents with a high nutrient load but also on the availability of structured habitats for attachment, protection, and optimal feeding. Finally, it brings forward a new understanding of selective trophic plasticity in facultative feeders, enhancing our broader knowledge of their ecological roles and adaptive strategies. In conclusion, this documented high-density aggregation occurrence of *H. cinerascens* underscores how hydrodynamic conditions and habitat complexity interactions can generate localized ecological population hotspots for benthic suspension-feeding organisms.

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First record of *Annella mollis* (Octocorallia) from Rodrigues Island, Western Indian Ocean

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Abstract. *Brihatee M, Marwyn A, Shakeel JY, Ashfaaq K, Maria RA, Homesha B, Ramkalam M, Deepeeka K, Beatriz CE, Yoshimi S, Hakim AA, Lalas JAA, Reimer JD, Wijayanti DP, Nascimento B, Ranjeet B. 2025. First record of* Annella mollis *(Octocorallia) from Rodrigues Island, Western Indian Ocean. Indo Pac J Ocean Life 9: 133-139.* Gorgonians octocorals inhabit environments ranging from shallow tropical reefs to deep and polar waters. A habitat-forming species, they contribute significantly to habitat structural complexity and biodiversity, yet their occurrence in the Western Indian Ocean (WIO) remains poorly documented. Rodrigues Island, in particular, has lacked formal records in gorgonian species. To address this gap, ecological surveys were conducted in April 2024 at seven fore-reef sites around Rodrigues using triplicate 10×5 m belt transects surveyed by SCUBA. Results showed that only one species, *Annella mollis*, was recorded and was restricted to two outer reef slope sites, Tombant Coco and Ti Paté, at depths of approximately 27 m. Mean densities were low (0.17±0.01 and 0.15±0.01 individuals m^{-2}, respectively), and colonies were dominated by medium size classes (76-150 cm), with few larger individuals. Colonies were attached to consolidated rocky substrates on steep slopes associated with higher coral cover relative to other surveyed sites. No gorgonians were observed at the remaining five, shallower sites. These findings provide the first baseline record of gorgonians from Rodrigues Island and contribute to the limited knowledge of octocorals in the WIO. Our observations highlight the apparent restriction of *A. mollis* to deeper reef slope habitats around the island and underscore the need for broader surveys, temporal monitoring, and complementary morphological and genetic analyses to better understand gorgonian diversity and ecological roles in the region.

Keywords: Gorgonian, habitat preferences, marine ecology, species distribution, zonation

Abbreviations: SCUBA: Self-Contained Underwater Breathing Apparatus, SIDS: Small Islands Developing States, WIO: Western Indian Ocean

INTRODUCTION

Gorgonians are colonial octocorals (class Octocorallia, phylum Cnidaria) characterised by a flexible internal axis and diverse branching morphologies, contributing to the three-dimensional structural complexity of reef habitats. Although once treated as a distinct group, recent phylogenomic analyses (McFadden et al. 2021) and taxonomic revisions (McFadden et al. 2021) have shown that gorgonians are polyphyletic. Nevertheless, the term remains useful to describe upright and branching octocorals as a functional ecological group (Bayer 1961). Octocorals, including gorgonians, are characterized by eight pinnate tentacles surrounding each polyp (Bayer 1961) and the colonies display diverse morphologies such as bushy, branched, whip-like, and fan-shaped forms (Fabricius and Alderslade 2001; Panero et al. 2023). These suspension feeders rely on ocean hydrodynamics to capture particulate and dissolved organic matter, including microscopic plankton (Ribes et al. 1999; Al-Marayati and Edmunds 2018), and occur from shallow tropical reefs to deep waters exceeding 1500 m, where they often serve as foundation species (McFadden et al. 2010). Gorgonians enhance the spatial heterogeneity of reef systems and contribute to marine biodiversity as components of Marine Animal Forests (Abeytia et al. 2013; Rossi et al. 2017). Beyond their ecological importance, they are valued for producing bioactive compounds (Häder 2021), serving as bioindicators of metal pollution (Velayutham et al. 2003), and attracting recreational divers (Cebrian et al. 2012; Renfro and Chadwick 2017).

Their distribution and morphology are shaped by multiple environmental factors, including depth, current, and habitat structure, as well as the presence or absence of symbiotic zooxanthellae (Sánchez et al. 2019). Gorgonian abundance often increases with depth, where reduced competition with scleractinian corals and suitable substrates promote growth (Panero et al. 2023). Assemblages in deeper habitats commonly include fan-shaped species (Rodríguez-Lanetty et al. 2003). Hydrodynamics influence both distribution and colony morphology, with current strength affecting orientation and feeding efficiency (Rowley 2018; Panero et al. 2023), while site-specific variation in water flow and reef topography can shape assemblage composition (Sánchez et al. 1997).

Like many ecosystem engineers and habitat-forming taxa, gorgonians face increasing pressures from rising sea temperatures, pollution, and disease outbreaks (Tignat-Perrier et al. 2022; Bellin and Rossi 2024; Rovira et al. 2024). Although some species exhibit greater resilience than scleractinian corals, they remain vulnerable to environmental stressors and may experience declines in abundance and health under worsening ocean conditions (Sánchez et al. 2019). Many gorgonians are also considered components of Vulnerable Marine Ecosystems (VMEs), as defined by the FAO, underscoring their ecological importance and the need for conservation (FAO 2009).

Despite their ecological and structural importance, most studies on gorgonian distribution have focused on the Caribbean (Kahng et al. 2010). Knowledge from the Indo-Pacific, particularly the Western Indian Ocean (WIO), remains scarce (Pérez et al. 2016). Rodrigues Island, a small volcanic island in the Republic of Mauritius and part of the Small Island Developing States (SIDS) and is surrounded by extensive coral reefs yet lacks any published record of gorgonians. These organisms are not currently included in reef monitoring programs despite the island's reliance on marine ecosystems for tourism and fisheries. Given their ecological significance and vulnerability to environmental change, establishing baseline data for gorgonians in Rodrigues is essential. This study provides the first formal record of gorgonians around Rodrigues Island, documenting the presence, distribution, and size classes of *A. mollis* from fore-reef slope habitats offering a baseline for gorgonian occurrence in the region and highlights potential habitat conditions associated with their presence. This preliminary dataset establishes a foundational reference point for Rodrigues Island and contributes to the broader understanding of octocoral biodiversity in the Western Indian Ocean.

MATERIALS AND METHODS

Study sites

Rodrigues Island, part of the Republic of Mauritius, is located in the Western Indian Ocean (WIO), approximately 600 km northeast of the main island of Mauritius (19.7245°S, 63.4272°E), near the boundary of the southern hemisphere's tropical belt. The island is surrounded by about 90 km of fringing reefs that enclose a shallow lagoon (Soondur et al. 2023).

Distribution surveys

Seven fore-reef sites were surveyed around Rodrigues Island between 22 and 25 April 2024 (Figure 1). The surveyed sites (Table 1) ranged between 9 to 28 m depth. At each site, a single dive was conducted within recreational SCUBA depth limits. The sites were selected to represent the typical depth range and reef slope habitats where gorgonians are commonly found and that can be safely surveyed using SCUBA. Depth was limited to approximately 30 meters to comply with SCUBA safety and no-decompression limits, which allowed sufficient bottom time for comprehensive belt-transect surveys while ensuring diver safety. The number of sites was constrained by logistical feasibility and environmental conditions during fieldwork, reflecting the exploratory nature of this preliminary baseline study. We acknowledge that this limited spatial coverage represents a constraint of the study design and recommend that future research expand sampling to additional sites and deeper reef zones to capture broader habitat variability.

At each site, three belt transects measuring 10×5 m were laid parallel to the reef slope, resulting in a total surveyed area of 150 m² per site (Abeytia et al. 2013). All visible gorgonian colonies within each transect were counted and measured using a 3 m fibreglass tape measure. Colony height was recorded from the base to the farthest tip of the tallest branch, following standard protocols (Camps-Castellà et al. 2024). Each colony was then assigned to one of four size classes: 0-75 cm, 76-150 cm, 151-225 cm, and 226-300 cm, to enable comparison of colony size distributions between sites. Hard coral cover was also assessed at each site using the Line Intercept Transect (LIT) method (English et al. 1997) along the same transects used for gorgonian surveys, allowing for comparable habitat description.

Table 1. Coordinates and depth of the seven fore-reef slope sites surveyed around Rodrigues Island, Western Indian Ocean

Site name	Latitude (°S)	Longitude (°E)	Depth surveyed (± SE)
Antonio's Finger	-19.66111	63.43944	9±0
Aquarium	-19.66639	63.43694	12.8±0
Plateau Bénitier	-19.66722	63.43556	11.4±0
Ti Trou	-19.66250	63.43890	10.7±0
Couzoupa	-19.76250	63.46390	21.6±0
Tombant Coco	-19.70770	63.28520	27.4±0
Ti Paté	-19.63370	63.43740	27.1±0

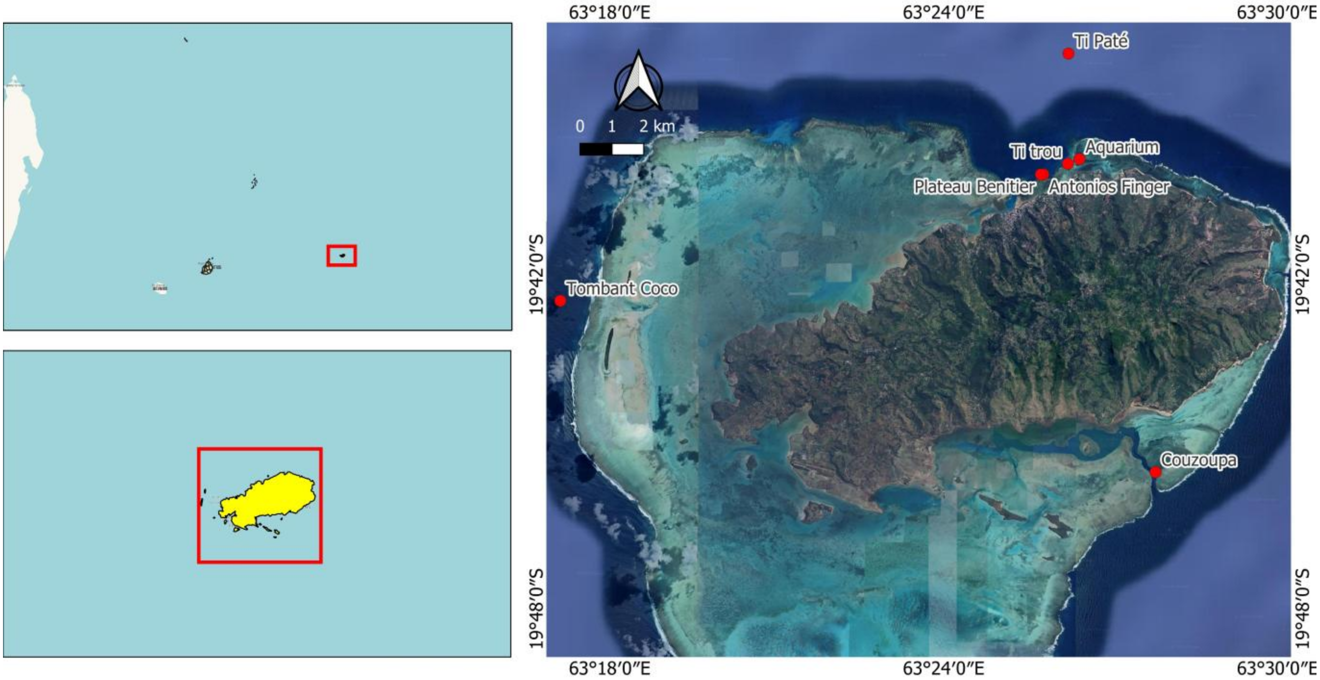

Figure 1. Map of Rodrigues Island with the study sites in the Western Indian Ocean

Taxonomic identification

Annella mollis was identified in-situ based on diagnostic macromorphological features and photographic records consistent with established descriptions (Nutting 1910; Bayer and Grasshoff 1995; Fabricius and Alderslade 2001). Colonies displayed a broad, planar fan structure with a regular, reticulate branching pattern and flattened, flexible branches. Polyps were arranged on both sides of the branches, characteristic of the genus *Annella*. Colony coloration ranged from pale yellow to light beige, occasionally with reddish-brown tints. These features are consistent with previous reports of *A. mollis* from the Indian Ocean and Western Pacific, including the coasts of East Africa, the Maldives, and the South China Sea (Goh and Chou 1996; Grasshoff 1999; McFadden et al. 2010). The species is known to occur primarily on deeper fore-reef slopes between approximately 12 and 50 m depth (Goh and Chou 1996; Pérez et al. 2016), which matches the depths (20-27 m) where colonies were observed at Rodrigues. The morphological consistency with these regional records supports the identification of the Rodrigues specimens as *A. mollis*.

Environmental and biological data collection

Depth (m) and temperature (°C) were recorded in-situ using a Cressi Goa diving computer to characterize site conditions and support qualitative comparisons of gorgonian occurrence and density. The Line Intercept Transect (LIT) method (English et al. 1997) was used to quantify scleractinian coral cover along each 10 m transect laid in the same area as the belt transects. Coral species intercepted by the transect line were identified in-situ and from photographic or video footage, and percentage coral cover was calculated for each site based on the cumulative length of coral intercepts relative to total transect length.

To describe the general environmental context of the surveyed reefs, seawater samples (n = 3) were collected at each site for analysis of chlorophyll-*a*, physico-chemical parameters, and nutrients. For chlorophyll-a, samples were taken at the same depth as gorgonian surveys and stored frozen until spectrophotometrical analysis to determine concentrations following Sandooyea et al. (2020), using wavelengths of 630, 647, 664, and 750 nm. For physico-chemical parameters, samples collected and were analyzed at the surface using a Milwaukee pH meter and a Milwaukee Digital Salinity Refractometer. Nutrient concentrations were determined following standard methods: nitrate by the cadmium reduction method (Margeson et al. 1980), silicate by the oxalic acid method (Strickland and Parsons 1968), and phosphate by the colorimetric method (Murphy and Riley 1962). Nutrient and chlorophyll-a data were used to provide general water-quality context for each site rather than for statistical analysis.

RESULTS AND DISCUSSION

Occurrence and habitat of *Annella mollis*

Throughout the survey, only a single gorgonian species, *A. mollis*, was recorded. The species was identified based on morphological identification. Colonies were observed at two of the seven fore-reef sites, Tombant Coco and Ti Paté, both located on exposed slopes facing the open ocean. Colonies were attached primarily to consolidated rock and rubble and were absent from sand substrates.

At Tombant Coco, the reef forms a stair-like cliff descending into deeper water, with colonies occurring from the upper steps (~15m) into deeper flanks. Colonies were mostly upright and scattered individually from few centimetres to several meters apart, although small clusters of up to three colonies were occasionally present.

At Ti Paté, colonies were observed on a dome-shaped rocky structure, concentrated along the rim and lower flanks. Colonies commonly grew oriented along the slope and exhibited a flattened fan-like morphology (Figure 2.D).

Across both sites, colonies were associated with diverse coral assemblages, including massive and encrusting forms (e.g., *Porites*, *Platygyra*, *Lobophyllia*, *Goniastrea*), as well as soft corals (Figures 2.E and F). All observed colonies appeared healthy, with no visible signs of tissue loss, necrosis, fragmentation, or overgrowth by epibionts. No sediment accumulation or biofilm coverage was observed on colony surfaces.

Distribution and environmental conditions

Annella mollis was recorded only at Tombant Coco and Ti Paté, both located on the outer reef slope at approximately 27 m depth. Colonies occurred at low densities of 0.17±0.01 and 0.15±0.01 individuals m^{-2}, respectively. Environmental characteristics for all seven sites are summarized in Table 2. The two sites with gorgonian presence were among the deepest surveyed and shared similar conditions, with in-situ temperatures of 28°C, salinity of 35 ppt, slightly alkaline pH values (8.19-8.25) and relative high coral cover (≈28-29%).

In comparison, the remaining five sites, ranging from 9 to 22 m depth, generally exhibited lower coral cover (≤7%), similar or slightly higher temperatures (29-31°C). Salinity values were comparatively similar (35-36 ppt) and pH was marginally lower (7.7-8.1) at these sites. Nutrient concentrations, including silicate, phosphate, and nitrate, varied widely but showed no consistent trend across the island. Overall, colonies of *A. mollis* were observed only at the deeper, outer-slope sites characterized by stable temperature, moderate alkalinity, and higher coral cover, while absent from shallower or nearshore reefs (Table 2).

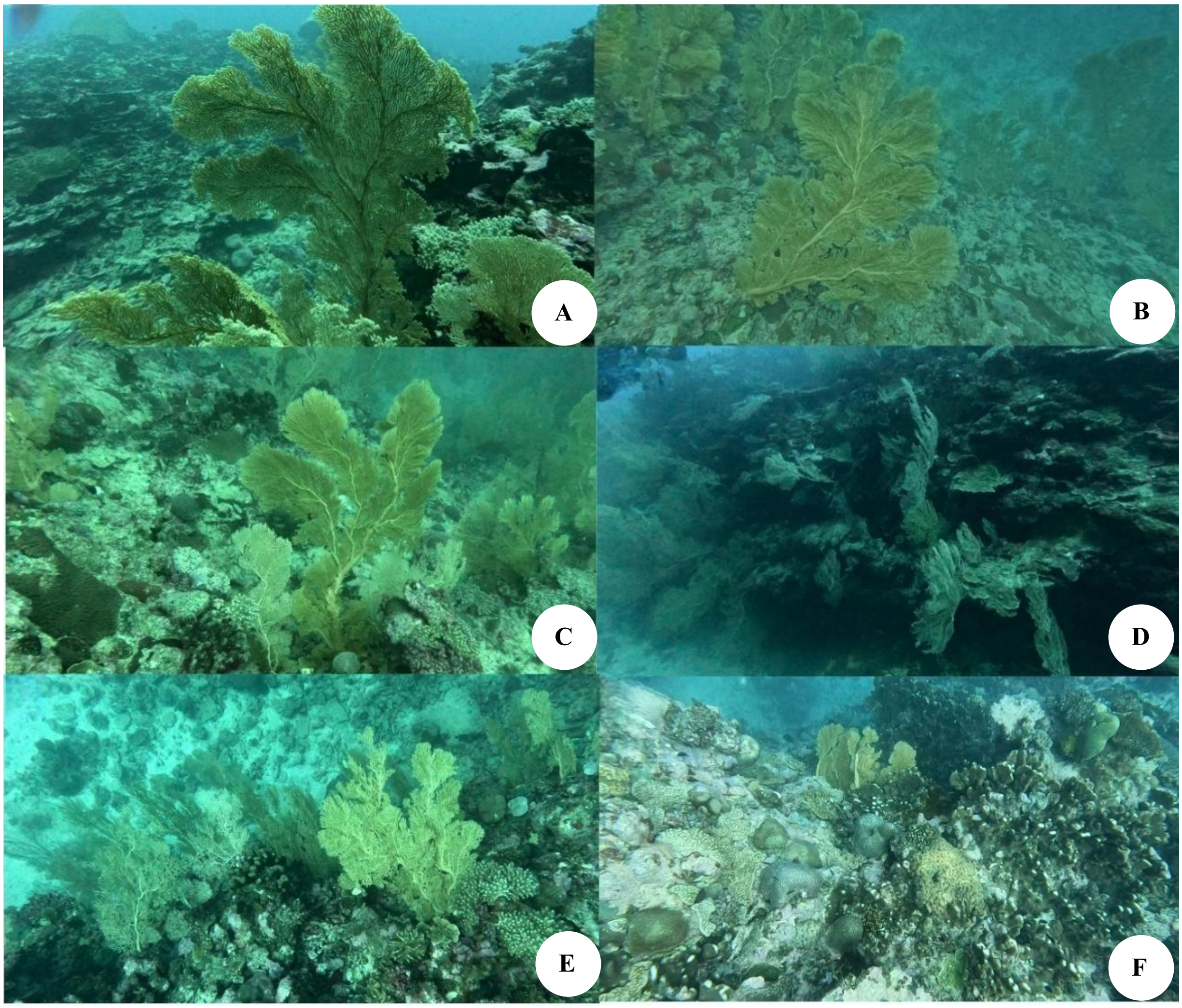

Figure 2. *Annella mollis* observed at Rodrigues Island, Western Indian Ocean. A, D, E. Ti Paté and B, C, F. Tombant Coco

Colony size structure

At both Tombant Coco and Ti Paté, *A. mollis* colonies were distributed across three size classes (0-75 cm, 76-150 cm, and 151-225 cm), with no colonies exceeding 225 cm in height at Ti Paté and only one large colony (>225 cm) recorded at Tombant Coco (Figure 3). The majority of colonies belonged to the 76-150 cm class, representing 9 colonies at Tombant Coco and 10 at Ti Paté, followed by smaller colonies (0-75 cm). Larger colonies (151-225 cm) were observed at both sites but were more frequent at Tombant Coco (8 colonies) than at Ti Paté (3 colonies). Mean colony height was approximately 120 cm at Tombant Coco and 110 cm at Ti Paté. Overall, *A. mollis* populations at Rodrigues were dominated by medium-sized colonies, with few individuals in the largest size class.

Discussion

This study documented for the first time records, as well as density, and size structure, of shallow-water gorgonians around Rodrigues Island. Only a single species, *A. mollis*, was recorded, restricted to two fore-reef slope sites, Tombant Coco and Ti Paté. These represent the first records of gorgonians from Rodrigues. *Annella mollis* is a reef-associated gorgonian distributed across the tropical Indian Ocean and Western Pacific, typically inhabiting deeper reef slopes exposed to strong tidal currents (Goh and Chou 1996). As an azooxanthellate species, it relies entirely on plankton and dissolved or particulate organic matter for nutrition (Sánchez et al. 2019).

In this preliminary survey, *A. mollis* was only observed at deeper reef slope sites of ~27 m with relatively higher scleractinian coral cover and diversity, and the species was absent from shallower, more sediment-impacted and less structured sites. This pattern aligns with ecological principles of habitat specialization and flow-mediated resource acquisition: strong currents enhance food delivery for suspension feeders, while mesophotic depths reduce competition from scleractinian corals, resulting in higher gorgonian abundances and colony sizes (Rodríguez-Lanetty et al. 2003; Pérez et al. 2016; Panero et al. 2023). Observations of colonies growing perpendicular to reef slopes at Ti Paté are also consistent with reports of gorgonian orientation with currents to optimize suspension feeding (Rodríguez-Lanetty et al. 2003). Preliminary statistical analyses indicate positive associations with depth, coral cover, and reef rugosity, although limited site replication precludes fully robust inference. Other environmental factors, including lower temperature (25-28°C), optimal pH (>8.0), and moderate salinity (32-37 ppt), may further favour *A. mollis* persistence at these sites. Sites closer to land or riverine input (Antonio's Finger, Aquarium, Plateau Bénitier and Ti Trou), with higher sedimentation or elevated nitrate levels, were devoid of gorgonians, suggesting sensitivity to water quality and turbidity (Yoshioka 2009; Tseng et al. 2011).

Colony size distributions were dominated by medium-sized individuals (76-150 cm), with few larger colonies. This pattern is consistent with observations from other Indo-Pacific sites, in which deeper habitats supported large fan-shaped species such as *A. mollis* (Goh and Chou 1996; Panero et al. 2023). The orientation of colonies perpendicular to the slope at Ti Paté is consistent with current-mediated feeding strategies. Low densities and restricted distribution likely reflect a combination of natural patchiness, environmental constraints, and sampling limitations, as only seven sites within a limited depth range were surveyed.

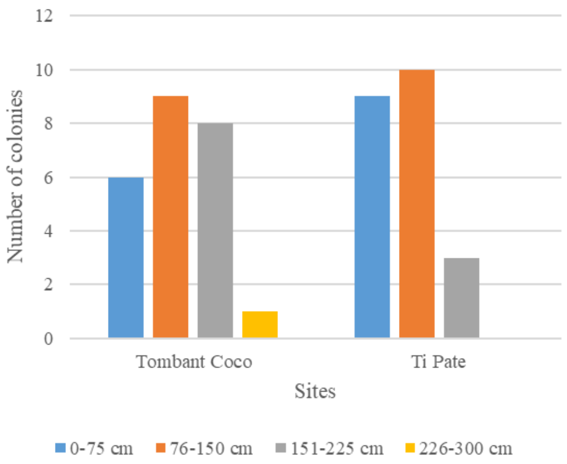

Figure 3. Size class distribution of *Annella mollis* colonies at the two sites where gorgonians were observed at Rodrigues Island, Western Indian Ocean

Table 2. Mean environmental and biological variables (±SE) across seven fore-reef sites at Rodrigues Island, Western Indian Ocean. *Annella mollis* was recorded only at the two deepest sites (Tombant Coco and Ti Paté), which exhibited greater coral cover and diversity compared to shallower sites

Site	Coral cover (%)	Coral diversity (H′)	Gorgonian density (ind·m⁻²±SE)	Temp. (°C)	pH	Salinity (ppt)	Silicate	Phosphate	Nitrate
Tombant Coco ✓	28.9	0.86±0.33	0.12± 0.01	28	8.25±0.00	35.00	2.32±0.22	1.95± 0.82	0.02±0.004
Ti Paté ✓	28.6	0.90±0.33	0.15±0.01	28	8.19±0.08	35.00	8.77± 2.82	2.05±0.86	0.02±0.005
Antonio's Finger ✗	0.12	0	0	30	7.80±0.00	35.00	5.43± 0.25	9.42± 5.74	-
Aquarium ✗	0.33	0	0	29	7.70±0.00	36.00	2.96±0.42	0.07±0.08	0.02±0.01
Plateau Benitier ✗	5.57	0.75± 0	0	30	7.80±0.00	36.00	1.68±0.31	0.28± 0.21	0.57±0.11
Ti Trou ✗	7.27	0.97±0	0	30	7.80±0.00	35.00	2.90±0.66	0.04± 0.05	0.09±0.04
Couzoupa ✗	27.63	0.93±0	0	31	8.10±0.00	35.00	1.12±0.44	0.39± 0.76	0.40±0.21

Note: Nitrate data were unavailable for Antonio's Finger due to sample loss during processing

Environmental conditions at the Rodrigues sites likely influenced the restricted distribution of *A. mollis*. Sites with higher pH (>8.0) supported gorgonian presence, consistent with previous findings that mesophotic gorgonians favour slightly alkaline conditions (Venn et al. 2013). Moderate salinity (32-37 ppt) was also associated with *A. mollis* occurrence, whereas sites with higher salinity lacked gorgonians, reflecting the species' vulnerability to abrupt salinity changes (Bayer 1961). Nutrient concentrations appeared to play a role in local gorgonian densities: sites with higher nitrate levels tended to have lower densities, suggesting that excessive nitrate may negatively affect growth or settlement, while weak positive associations were observed with silicate and phosphate, potentially reflecting their contributions to primary productivity and the availability of particulate organic matter for suspension feeding (Bellin and Rossi 2024). These observations indicate that water chemistry, including pH, salinity, and nutrient concentrations, interacts with depth and structural habitat characteristics to influence *A. mollis* distribution on Rodrigues mesophotic reefs.

These results provide the first baseline record of gorgonians at Rodrigues Island and extend the knowledge of their distribution within the Western Indian Ocean. Given the ecological importance of gorgonians as suspension feeders and habitat-forming taxa (Ponti et al. 2014; Sánchez et al. 2019), further surveys are needed to better document gorgonians' distributions and ecological roles in Rodrigues reef communities.

In conclusion, this study provides the first formal records of gorgonians at Rodrigues Island, documenting a single species, *A. mollis*, at two fore-reef slope sites. Colonies occurred at low densities and were dominated by medium size classes. These findings highlight the restricted distribution of gorgonians in the surveyed areas and provide an important baseline for future research in the Western Indian Ocean.

Although this study bridges a significant knowledge gap in the biodiversity of Rodrigues Island, several limitations should be acknowledged. The survey encompassed only seven sites and was limited to depths shallower than 30 m, providing a spatially restricted snapshot of the island's gorgonian assemblages. Future studies should therefore broaden spatial coverage to include deeper reef slopes and additional habitat types, while incorporating repeated surveys to capture temporal dynamics to assess long-term population stability.

Furthermore, species identification relied exclusively on macromorphological characteristics visible during in-situ observations. While diagnostic characters clearly matched *A. mollis*, the absence of sclerite and molecular analyses introduces some uncertainty. Future research incorporating genetic tools (e.g., COI barcoding) and detailed morphological examinations will be essential to confirm species identity and refine regional taxonomic records. Such integrative approaches, combined with expanded spatial and temporal surveys, will be essential to understanding the diversity, ecology, and resilience of gorgonians at Rodrigues, and to informing conservation strategies across the Western Indian Ocean under changing environmental conditions.

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Conservation under warming ocean conditions for endemic corals and reef fishes of Rodrigues Island, Republic of Mauritius

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Abstract. *Munbodhe V, Bhagooli R. 2025. Conservation under warming ocean conditions for endemic corals and reef fishes of Rodrigues Island, Republic of Mauritius. Indo Pac J Ocean Life 9: 140-155.* Ocean warming has accelerated coral-algal phase shifts, threatening reef biodiversity and ecosystem functions. This study assessed coral reef conditions across 14 sites around Rodrigues Island, Mauritius, including four Marine Protected Areas (MPAs) and ten Non-Protected Areas (NPAs), surveyed from November 2019 to December 2020. Coral cover, macroalgae, and substrate covers were quantified using underwater visual censuses and 15 quadrats per site (~4 m^2 each). Live coral cover in MPAs was 2.5 times higher than in NPAs, with significant differences in benthic composition (GLM–Poisson, $p<0.001$). Significant differences in live corals, macro-algae, and soft coral covers were observed between MPAs and NPAs, GLM-Poisson Distribution, $p<0.001$. The MPA harbored 2.5-fold more live corals than NPAs. Relatively low coral genera richness was noted in the no-take marine reserves (Pielou's Evenness Index, $J=0.31$ and Simpson Dominance, $D=0.65$) as compared to multiple use MPAs ($0.65<J<0.96$) and NPAs ($0.94<J<0.83$). Of the 150 coral species recorded, 47 were from the genus *Acropora,* which mostly occurred in the MPAs. The MPAs demonstrated significantly higher reef structural complexities than the high macroalgal and rubble covers in the NPAs, ANOVA Post-hoc, $p<0.007$. No endemic coral, *Acropora rodriguensis*, was observed at the surveyed sites, while *Pomacentrus rodriguensis*, the endemic reef fish, was dominant in algal-dominated NPAs. The presence of regionally and nationally endemic species highlights Rodrigues as a biodiversity hotspot requiring strengthened reef management. This study provides critical baseline data for coral reef resilience and underscores the need for genetic and long-term ecological monitoring to support ecosystem-based conservation in a warming ocean.

Keywords: *Acropora*, coral species, endemic and rare, reef fishes, marine protected area

Abbreviations: HC: Hard Cover, GLM: General Linear Model, MA: Macroalgal cover, MPAs: Marine Protected Areas, Npas: Non-Protected Marine Areas, RUB: Rubble, SC: Soft coral cover, SIDS: Small Island Developing States

INTRODUCTION

Coral reefs are vital for being one of the world's most productive ecosystems (Graham et al. 2006). Besides providing ecosystem functions, coral reefs play a fundamental role in supporting fisheries and the tourist industries (Bellwood et al. 2004; Obura et al. 2019). Despite being recognized for its diverse socio-economic benefits, coral reefs have been continuously undergoing structural and functional modifications due to human disturbances (Hughes et al. 2017) which are further exacerbated by prolonged marine heating (Reimer et al. 2024). Overall, the three-dimensional complex structure corresponds to the wide range of habitats extending from food, shelter, to nursery ground to associated biomes (Martinez and Altvater 2024). As such, one hectare of coral reefs is valued at about $352,000 for one year of economic and ecological goods and services (Fezzi et al. 2023).

Yet, the reef functions are severely compromised (Hughes et al. 2018) for instance, phase shifts from coral to algal dominated habitat and reduction in reef structural complexity give rise to (i) the loss of reef fish biodiversity (Darling et al. 2017) and (ii) reduced coastal protection (Spalding et al. 2014) and reduction in fisheries, wave attenuation and carbon sequestration (Powell et al. 2020). Persistent overfishing has been amongst the leading stressor resulting in the collapse of many of the world's fisheries (Gaylord et al. 2005). The failure of traditional fisheries management including maximum sustainable yield, fisheries quotas, amongst others led to the emergence of ecosystem-based management in the form of marine reserves (Long et al. 2015). With growing knowledge in reef community structural changes, the establishment of marine reserves became instrumental to protect, maintain, and restore most of the targeted species and other reef associated organisms with the hope of mitigating some of the anthropogenic threats (Lester et al. 2009; Eli et al. 2025).

Likewise, the reefs of the Indian Ocean are also exposed to both human-induced disturbances and the warming environment. Studies of 822 reefs of the Western Indian Ocean have shown that post-1998 bleaching has claimed the loss of over 25% of the coral functionalities in the region due to significant loss of live coral covers (Obura et al. 2019), while recent findings suggest that there has been a considerable increase in rubble and macro-algal dominance (Elliott et al. 2018; Ricot et al. 2025) with severe loss in coral diversity (McClanahan and Muthiga 2020). Furthermore, the latest photo-physiological experiment on common corals from the Mascarene Plateau from Saya de Malha, St Brandon, and Mauritius described the degree of vulnerability of reefs under anthropogenic influences to prolonged climate variabilities (Munbodhe et al. 2025). Situated in the easternmost tip of the Mascarene Plateau, Rodrigues Island, considered a marine biodiversity hotspot, harbors endemic coral, *Acropora rodriguensis*, and endemic reef fish, *Pomacentrus rodriguensis*. However, limited ecological information is available on their distribution and abundance.

Along with increasing population and intensifying tourism industry, the Rodrigues Island, a Small Island Developing State (SIDS), is continuously threatened by the climatic challenges (IPCC 2023). Subsequently, the reefs are exposed to unprecedented impacts of the warming ocean and the sea level rise (Doorga et al. 2025). The mounting pressures on coastal fisheries, compounded by significant impact from thermal-driven coral bleaching and coral diseases (Jogee et al. 2025), further fragilize the benthic and fish community structures (Ricot et al. 2025; Moreno-Borges et al. 2025). Moreover, ongoing reef structural alteration profoundly reduces reef functionality, coral reef resilience (Wu et al. 2024), and biodiversity functions, leading to a critical reduction in certain specialist reef fish abundance (Zhang et al. 2025). In view of the escalating ecological threats and biodiversity loss globally, this study attempts to generate vital scientific data on the occurrence and abundance of the endemic coral, *A. rodriguensis,* and endemic reef fish, *P. rodriguensis,* along with targeted rare coral and reef fishes, while evaluating the reef status of understudied shallow backreefs and mid-lagoons at 14 selected sites within the Marine Protected Areas (MPAs) and Non-Protected Areas (NPAs) of the Rodrigues Island. It is therefore hypothesized that by virtue of its enhanced reef management strategies, Marine Protected Areas (MPAs) sustain higher live coral coverage and coral diversity than Non-Protected Areas (NPAs), and that endemic and rare species occur more frequently in structurally complex, low-impacted reef habitats.

MATERIALS AND METHODS

Study area

Rodrigues Island, a sovereign part of the Republic of Mauritius, is surrounded by a fringing reef, which forms a continuous band approximately 90 km long. The reef encloses a shallow lagoon of 240 km^2, Table 1, (twice the area of the island). It is situated on a submarine spur lying eastward of the main Mascarene Plateau and is the smallest of the Mascarene Islands (108 km^2 which lies on a submarine rise between the Mascarene and St Paul-Chagos ridges (Duncan and Hargraves 1990). The island lies 570 km to the East of Mauritius, sits on an east-west axis, along which runs a spine-like mountain range approximately 600 meters above sea level. It is volcanic in origin and is dominated by a central ridge which crosses the island almost throughout from the East to the South-west, over a distance of about 10 km, tapering off in the West into a calcareous coral plain (Thébault et al. 2009). It is surrounded by a large fringing reef that encloses 240 km^2 of lagoon area with 18 small islets. Rodrigues is the only Mascarene Island with extensive limestone deposits (Middleton and Burney 2013). The main coastal features include basaltic rock shores, coral reefs, lagoons, sand beaches, estuaries, wetlands, and mangroves. It has a population density of about 40,000 is largely dependent on agriculture and fishing (about 90% of the workforce) (Pasnin et al. 2016)

The South East Marine Protected Area (SEMPA) zoning has been subdivided into a no-take marine reserve and several multiple-use Marine Protected Areas (MPAs), and key planning documents have been drafted for successful management, including several studies and the development of SEMPA's Management Plan (Pasnin et al. 2016). SEMPA was designed to be a showcase of participatory MPA management. SEMPA includes both Trou Blanc, the no-take and the multiple-use MPAs, which are separated by the natural reef opening giving rise to a channel. Important global benefits were generated through the creation of SEMPA and its strengthened management through participatory approaches. A main challenge in SEMPA was noted, which was recognized as the lack of local capacity in MPA management (Pasnin et al. 2018). In addition, 4 other Marine Reserves were gazetted in 2007 in the northern and north-western sectors of the lagoon and occupy ~20 km^2.

The four Marine Reserves (MR) are Riviere Banane, Anse aux Anglais, Grand Bassin, and Passe Demi Marine Reserves. Riviere Banane MR is situated in the northeast of the island, which covers an area of 1.5 km^2 of shallow lagoon extending to the fore reef, which has been reported as degraded (Pasnin et al. 2018). Anse aux Anglais MR is located in the north most of the island with an area of 1.5 km^2 with relatively high coral cover in the reef slope (Pasnin et al. 2018) while Grand Bassin MR is located in the northwest with an area of 14.1 km^2 with low coral cover in the backreef as compared to about 46% coral cover in the reef slope and Demi Passe MR covers an area of 7.2 km^2 with relatively low coral cover (Pasnin et al. 2018). Fenner et al. (2004) reported the occurrence of the endemic coral *A. rodriguensis* and the endemic reef fish *P. rodriguensis* and *Amphiprion chrysogaster* at Riviere Banane and Anse aux Anglais Marine Reserves, Mauritius.

Survey sites

All surveys conducted in the lagoons of Rodrigues Island were covered under the authorization obtained from the Commission for Agriculture, Environment, Forestry, Fisheries, and Marine Parks, Rodrigues Regional Assembly, Republic of Mauritius. Due to the limited number of field days and boat availability, only 14 sites were assessed, whereas on 17 November 2019, contact with boat operators, diving sites, and the fishermen community was established, and the site selection was done based on accessibility, along with a stock-taking exercise. However, all the 14 sites were surveyed from 17 to 20 December 2020 which included one no-take MPA at Trou Blanc bordering the reef opening (channel) in the south-east along with three multiple-use MPAs, namely, Vas Brulee (south-east), Riviere Banane (East) and Anse aux Anglais (north), Figure 1. In addition, 10 non-protected lagoons and backreef areas were also surveyed viz. Trou Mullet I (south-east mid-lagoon), Gros Pot, Bar Chirurgien, Trou Mullet II (south mid-lagoon), La Butte (west backreef), La Ferme (North-west backreef), Baie aux Huitre, Terre Rouge, Cavern Provert, and Grand Baie, the northern backreef sites (Figure 1).

Research strategy and sampling design

Extensive island-wide field surveys were carried out at 14 sites. Irrespective of the coral diversity and reef structural complexity, sites were selected based on site accessibility, and random surveys for benthic assessment were done randomly (McClanahan et al. 2005), conversely to coral and targeted reef fish search. The survey area varied from backreefs (<1m deep) to mid-lagoons (>2 m deep), ranging from 0.1 to 0.2 km^{2,} which included shallow reefs and larger lagoons/mid-lagoons in both Marine Protected Areas (MPAs) and non-managed sites, Non-Protected Marine Areas (NPAs). Three sets of data were compiled from each ecologically surveyed site. Firstly, a stock-taking exercise of each site was done by collecting substrate cover data for about 30 minutes of snorkeling randomly so as to cover a wider area (McClanahan et al. 2005), as opposed to LIT and Photo-quadrants, which are more time-consuming and limited to a pre-defined area; these methods are suited best for long-term reef monitoring (Urbina-Barreto et al. 2021; Carneiro et. al 2024). The Visual Census technique was used for approximately 90 minutes for the search for endemic and rare coral and reef fishes, as well as to photograph all coral colonies encountered during that period, providing insight into the different coral diversity.

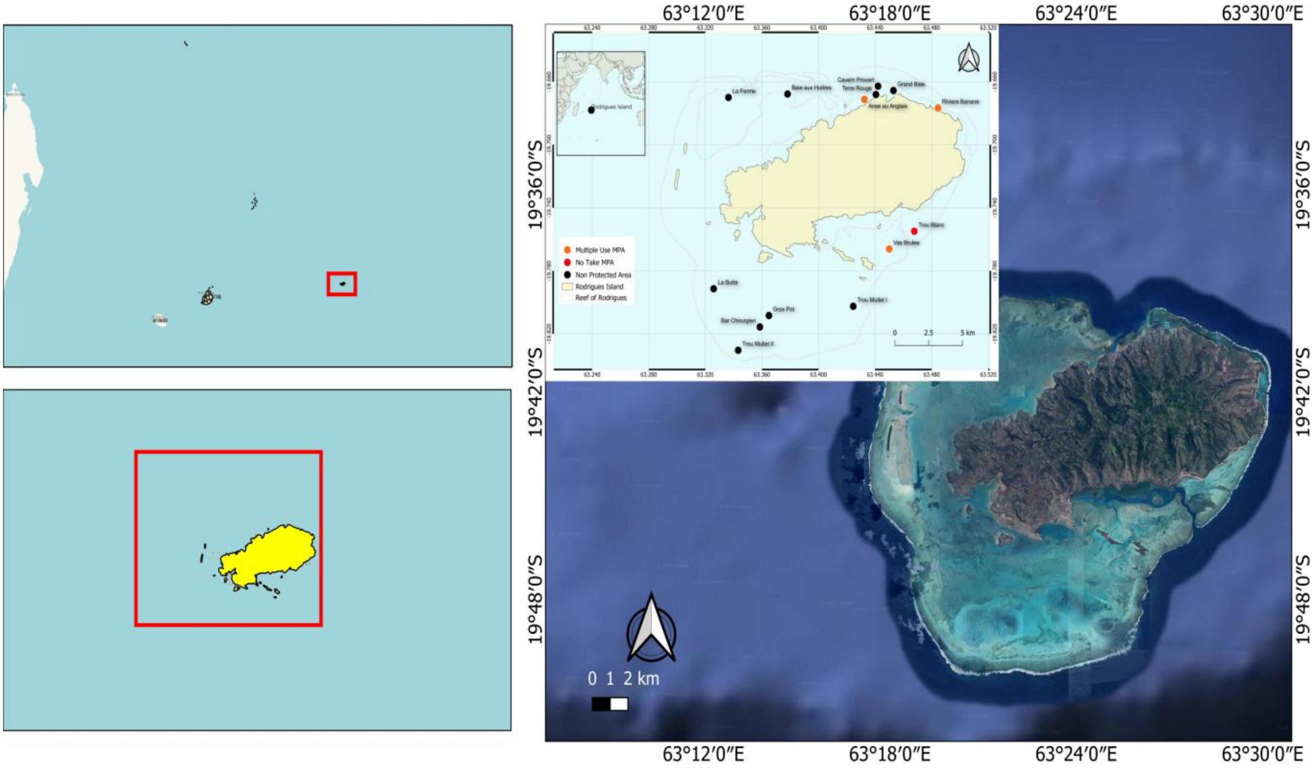

Figure 1. The geo-referenced map of Rodrigues Island, a sovereign part of the Republic of Mauritius, shows the geo-location of the no-take and the multiple-use MPA, and the NPA of the 14 surveyed. Note: Geo-referenced map indicates the location of each site as per the respective GPS coordinates recorded during the surveys

Table 1. Characteristics of Rodrigues Island (Mauritius) and reef management framework

		Rodrigues Island
Geomorphology	Longitude	19°40'S
	Latitude	63°20'E
	Landmass	108 km²
	Coastline	322 km
	Lagoon area	240 km²
	Reef type	Fringing
Climate		Mild tropical
	Temperature	20.4°C-24.7°C
	Wind	Prevalent Southeast Trade Wind
	Mean Annual Rainfall	about 1140 mm
Demography	Population size	41,000
Economic contribution	Main activities	Fisheries activities: octopus fisheries as a major fisheries activity, along with large net and handline fisheries Tourist industry
Reef Management	Marine Protected Areas	5 Fisheries Reserved Areas, 4 Marine Reserves, and a multiple-use Marine Protected Area in the south-east of Rodrigues (SEMPA) with a strict no-take zone
Legal Framework	Legislation and Regulation	Fisheries Act 2023 Closed Season for Net fishing starting from the 1st day of October of one year to the last day of February the following year Fisheries and Marine Resources (fishing of octopus) (Amendment) Regulations GN No. 138 of 2020 Fisheries and Marine Resources (Fishing of Sea Cucumbers) (Amendment) Regulations 2020, the Toxic Fishes Regulations 2004. Prohibition of Removal of Coral and Seashell Regulations 2006. The Undersized Fish Regulations 2006. Fishing of Sea Cucumbers Regulations 2008, 2009 & 2012. Prohibition of the Use of Hooks of Small Size Regulations 2011 The Marine Protected Areas Regulations 2001.

Note: Source: Statistics Mauritius, Government of Mauritius, https://statsmauritius.govmu.org/SitePages/Index.aspx

Reef benthic communities survey

This study focused on random data collection of benthic coverage with respect to hard coral cover, soft coral cover, and macroalgal assemblages. The underwater visual census method was used to evaluate the benthic communities. The benthic cover data collection was conducted by estimating the percentage of the live hard coral cover (HC), soft coral cover (SC), the macroalgal cover (MA), and rubble (RUB) at each selected site. Prior to data collection, each site was geo-referenced. At each selected site, a diver, after getting into the water, swims for about 30 seconds with closed eyes randomly, and then the diver after opening the eyes, selects an imaginary quadrat of approximately 4 m^2. After demarcating the quadrat, the observer then scans the benthic cover and records the estimated % cover of the attributes (HC, SC, MA, and RUB) within the imaginary quadrat. Due to time constraints and to avoid limitations in the area covered, unlike the Line Intercept transect, this underwater visual census exercise was randomly repeated 15 times for each site over a wider range so as to maximize area coverage of the relatively larger and heterogenous reefs. However, after every quadrat, the observer closes their eyes and makes five kicks to start another quadrat, making the sampling as unbiased as possible. As such, 15 random quadrats per survey site were used to estimate the % live coral cover of that particular site (McClanahan et al. 2005), covering a wide area, conversely to Line Intercept Transect or photoquadrants (Jokiel et al. 2015). The imaginary quadrat was more time-efficient both in terms of data collection and data inputs, whereby within 30-45 minutes, in-situ data were collected.

Coral inventory

A list of coral species occurring at each site was compiled based on surveys conducted between 2018 and 2021 by snorkeling the entire lagoon. Over 15,000 photos of the multitude of coral colonies were taken, including close-up shots using the Canon D30 (109×68×28 mm; 4.29×2.68×1.1″) for coral identification at the species level using Allen and Steene (1994), Veron (2000), Moothien-Pillay et al. (2002) and WORMS (2024). The survey was conducted in the near-shallow, mid-lagoon, and MPAs where the coral colonies were most abundant; nevertheless, the near-shore area was also inventoried, which harbored mainly massive *Porites* and occasional branching *Acropora* with macroalgal assemblages and rubbles on the sandy bottom.

Coral diversity, data generation, and coral identification

A high-resolution photographic underwater camera (Canon PowerShot D30 Full HD 21.1 Mega Pixel) was used to capture individual coral colonies as well as to take close-up photos, which were later used for morphological identification and quantification of the coral genera at each selected site. Over 400 to 500 photos per site were captured for image analysis. The number of colonies of the listed corals (genus–level) was recorded during the survey. Image analysis, i.e., coral identification to species level, was performed using Allen and Steene (1994), Veron (2000), and Moothien-Pillay et al. (2002). Differences and similarities in the coral morphologies, i.e., massive, tabular, branching, corymbose, encrusting, and foliose, were observed, and close-up characteristics of the corals were compared with those of Veron (2000) and others. Closed-up characteristics of corals were mainly differences in corallites, axial and radial, branches thickness, tips, regularity for branching corals, while walls, budding stages, and paliform lobes were used to differentiate among *Favia*, *Favites*, *Montastrea*, and *Goniastrea* spp, whereas the depth, length, regularity, and continuity of valleys in *Lobophyllia*, *Euphyllia*, *Symphyllia*, *Platygyra*, *Leptoria* spp., and others. Coral diversity was quantified at the taxa level among 66 taxa to assess genus-level coral diversity and evaluate the coral structural dominance at each site (McClanahan et al. 2005). Over 6,000 photos were analyzed for the 14 sites.

Targeted species – Endemic and rare corals and reef fishes

Due to a lack of prior assessments on the endemic and rare corals and reef fishes, we evaluated the literature to identify rare and endemic species. Upon consultation with fishermen, coastal communities, and conservation organizations concerned with coral reefs, and after consideration of the literature and communication from diving communities, one endemic coral, *A. rodriguensis*, and one endemic reef fish, *P. rodriguensis*, from Rodrigues Island were selected as endemic species for the study. The list of regionally endemic and rare coral and reef fish species was compiled from the literature. The regionally endemic coral species were *Acropora branchi, Horastrea indica,* and *Pocillopora indiania,* while *Seriatopora hystrix*, *S. calendrium,* and *Stylophora pistillata* were identified as rare coral species. The regionally endemic reef fishes that were identified as rare were *Abudefduf margariteus, Zebrasoma gemmatum, Ostracion trachys, Pomacentrus pikei*, and *Amphiprion latifasciatus* (anemone fish) (Table 2).

Statistical analyses

General Linear Model (GLM)-Poisson Distribution was used to compare the substrate covers of the MPAs and NPAs for Rodrigues, Jamovi (Version 5) Model Fit, $R^2=0.37$, $p<0.001$; Omnibus Tests, Management, Substrate and Management v/s Substrate p<0/001. One-way ANOVA- Welch's Test, $p<0.005$, Shapiro-Wilk Test for normality, $p>0.05$, were used to assess the variation in the distribution of coral genera, while ANCOVA, Post-hoc Bonferroni corrected, $p<0.05$, determined the coral species diversity and the dominance of *Acropora* species between the MPAs and NPAs. Shannon-Wiener (H), Simpson Diversity (D), and Pielou's Evenness (J) were used to determine the diversity of coral species harbored by the MPAs, mid-lagoon, and shallow-reef NPAs. The Q-GIS software was used to generate geo-referenced maps to demonstrate the site-wise benthic coverage and to show the occurrence and distribution of the coral genera, indicating the dominance of certain different corals in specific regions around Mauritius and Rodrigues, along with targeted species regionally and endemic rare coral and reef fishes.

Table 2. Summary on targeted coral and reef fishes for the study

List of endemic and rare coral species under study			
Scientific name	**Occurrence**	**Status**	**IUCN Red List**
Acropora rodriguensis (Pichon, 1980)	Shallow reef environment (Hardman et al. 2004)	Endemic to Rodrigues Island (Pasnin 2011)	**Status:** Not clearly documented; Data deficient, **Population:** Unknown
Acropora branchi (Riegl, 1995)	Indian Ocean, coastal region in the upper reef slope (Veron 2000)	Regionally Endemic Western Indian Ocean (Obura 2012)	**Status:** Data deficient, **Population trend:** Decreasing
Acropora clathrata (Brook, 1891)	Indo-Pacific, upper reef slopes, backreefs and fringing reefs (Veron 2000)	Occurs in the tropical and subtropical reef regions	**Status:** Data deficient, **Population trend:** Decreasing
Horastrea indica (Pichon, 1971)	Very rare coral, occurrence limited to sandy reef areas (Veron 2000)	Regionally endemic Western Indian Ocean (Obura 2012)	**Status:** Vulnerable, **Population trend:** Unknown
Pocillopora indiania (Veron, 2000)	Indian Ocean, coastal region in the upper shallow reef (Veron 2000)	Regionally Endemic Western Indian Ocean (Obura 2012)	**Status:** Vulnerable, **Population trend:** Unknown
Seriatopora hystrix (Dana, 1846)	Shallow reef environment (Veron 2000)	Occurs in the tropical and subtropical reef regions	**Status:** Vulnerable, **Population trend:** Decreasing
Seriatopora caliendrum (Ehrenberg, 1834)	Upper reef slope (Veron 2000)	Occurs in the tropical and subtropical reef regions	**Status:** Near Threatened, **Population trend:** Unknown
Stylophora pistillata (Esper, 1797)	Exposed reef fronts to shallow reef flats (Veron 2000)	Occurs in the tropical and subtropical reef regions	**Status:** Near Threatened, **Population trend:** Unknown

List of endemic and rare reef fish species under study			
Scientific and common name	**Occurrence**	**Status**	**Ecological niche**
Stegastes rodriguensis (Allen and Wright, 2003)	Inhabits reef areas, commonly found in *Acropora* dominated reefs (Fishbase.de)	Endemic to Rodrigues Island	Reef-associated and territorial
Stegastes pelicieri (Allen and Emery, 1985)	Inhabits rocky reefs, rubble substratum area in shallow and calm lagoon near crevices and holes (Fishbase.de; Terashima et al. 2001)	Endemic to Mauritius and Reunion Islands (Fishbase.de)	Reef-associated and non-migratory, Shallow lagoon/Reef flat
Amphiprion chrysogaster (Cuvier, 1830)	Inhabits reef areas, more specifically in sea anemone, *Hectaractis magnifica*, *Stichodactyla mertensii* (Fishbase.de)	Endemic to Mauritius (Fishbase.de)	Specialist – habitat specific, Shallow lagoon/Reef slope
Pomacentrus pikei (Bliss, 1883)	Inhabits rocky reefs, rubble substratum area in shallow and calm lagoon near crevices and holes (Fishbase.de; Terashima et al. 2001)	Distributed in the Western Indian Ocean, regionally endemic (Fishbase.de)	Reef-associated and non-migratory, Shallow lagoon/Reef slope
Stegastes limbatus (Cuvier, 1830)	Inhabits branching coral in the lagoon areas and exhibits territorial behaviour (Fishbase.de; Terashima et al. 2001)	Distributed in the Western Indian Ocean, regionally endemic (Fishbase.de)	Territorial reef-associated and non-migratory, Shallow lagoon/Reef slope
Ostracion trachys (Randall, 1975)	Occurs mainly in the outer reef between 15 to 30 m, found chiefly in holes and crevices (Fishbase.de)	Endemic to Mauritius and Reunion Islands (Fishbase.de)	Reef-associated and non-migratory, Outer reef
Abudefduf margariteus (Cuvier, 1830)	Inhabits coral and rocky reefs around lagoons and reef slopes (Fishbase.de; Terashima et al. 2001)	Distributed in the Western Indian Ocean (Fishbase.de)	Supposedly common in Mauritius
Zebrasoma gemmatum (Valenciennes, 1835)	Occurs mainly in the outer reef between 15 to 60 m, found chiefly in holes and crevices (Fishbase.de)	Distributed in the Western Indian Ocean, regionally endemic (Fishbase.de)	Reef-associated
Amphiprion latifasciatus (Allen, 1972)	Associated with the anemone *Stichodactyla mertensii.* Resides both lagoons and outer reef (Fishbase.de)	Distributed in the Western Indian Ocean, regionally endemic (Fishbase.de)	Specialist – habitat specific, Shallow lagoon/Reef slope
Pomacentrus agassizii (Bliss, 1883)	Inhabits lagoon and inshore coral reef areas (Fishbase.de)	Distributed in the Western Indian Ocean (Fishbase.de)	Reef-associated and non-migratory
Plectroglyphidodon randalli (Allen, 1991)	Inhabits lagoon and inshore coral reef areas (Fishbase.de)	Distributed in the Western Indian Ocean (Fishbase.de)	Reef-associated and non-migratory

Mapping

A free and open-source Geographic Information System (GIS) software, QGIS Software version 3.34.8-Prizren, was downloaded, available at QGIS.org, and used to create all the maps in this project. Data was acquired by downloading the required base map layers from MarineRegions.org, including various marine and coastal datasets consisting of the Indian Ocean, Mauritius, Rodrigues, and the reef of Mauritius/Rodrigues basemaps. All the downloaded files were downloaded in a compatible shapefile format as vector layers. The World Map was also used in this project to verify all the maps from MarineRegions.org.

The world map and the Coordinate Reference System (CRS) were imported into the project with the project's CRS correctly set. For all maps used in this project, the commonly used projection is WGS 84. Layers were arranged in the Layers Panel so that the base maps appear below any thematic layers. Symbology was applied by double-clicking on each layer in the Layers Panel to open the Layer Properties dialog, and appropriate symbology was chosen for each layer. For example, use different colors to differentiate between MPA and NPA as orange/red and black, respectively. Labels were customized using the callout option to allow labeling for sites without overlapping each other. In the Labels tab of the Layer Properties, options such as placement and rendering were constantly used to attribute all labels, sites, and graphs.

RESULTS AND DISCUSSION

Coral cover in the MPAs and NPAs

Overall, 14 sites within the lagoons of Rodrigues Island were surveyed for their substrate covers, which included hard coral (live), soft coral, macroalgae, and rubble. Of the surveyed sites, four were Marine Protected Areas (MPAs), of which Trou Blanc was a no-take MPA, and the three others were multiple-use MPAs, whereas the 10 remaining sites were areas open to fishing activities, Non-Protected Marine Areas (NPAs). Trou Blanc harbored the most live coral cover (mean: 60.33±6.04%, S.E) with hardly any macroalgae, 6.33±5.65% and 23.76±3.03% of soft corals and rubbles, respectively (Figure 2). Vas Brulee, Riviere Banane and Anse aux Anglais, the three multi-use MPAs had 34.74±4.85%, 33.33±4.01%, and 39.67±4.71%, respectively. The results further showed that Baie aux Huitres was the only NPA which had over 28.0% of live coral cover (28.67±4.74%) whereas the rest of the surveyed NPAs registered between 11.67 to 18.67% live coral cover with the highest macroalgal at Bar Chirurgien (71.33±2.99 %) followed by La Butte (70.67±2.84%) and Gros Pots (69.67±2.95%). Rubbles were dominant at Trou Mullet II (63.67±4.32%), followed by Terre Rouge and La Ferme (53.67±3.51% and 48.67±3.57%). It is noteworthy that Riviere Banane (multiple-use MPA) had almost two-fold rubbles (52.33±4.73%) than Vas Brulee (29.67±5.97%), followed by Anse aux Anglais, whereas denser macroalgal cover was recorded at Riviere Banane. The dominance of soft corals was more pronounced at Vas Brulee (33.33±6.07%) as compared to Trou Blanc with 16.33±5.66%), while the soft coral cover was negligible at Riviere Banane and Anse aux Anglais. Whereas Trou Mullet I had the most soft-coral coverage with 50.33±6.87%.

Significant differences in live coral, macro-algae, and soft coral covers were observed between MPAs and NPAs, whereas no significant difference in rubble dominance between the MPAs and NPAs was observed, Bonferroni Post-hoc Test, $p<0.001$, GLM -Poisson Distribution, Model Fit, $R^2=0.37$, $p<0.001$ (Table 3). Overall, the mean live coral cover within the MPAs was 41.92±2.8% whereas the NPAs registered 16.23 ± 0.93%. There was a visible dominance of macroalgae in the NPAs, with 48.57±1.88% compared to 12.75±2.45% in the MPAs. On the contrary, mean rubble was 32.50±2.60% and 30.13±4.73% in MPAs and NPAs, respectively (Figure 2).

Table 3. General Linear Model (GLM)-Poisson Distribution was used to compare the substrate covers of the MPAs and NPAs, Model Fit, $R^2=0.37$, $p<0.001$; Omnibus Tests, Management, Substrate and Management v/s Substrate $p<0.001$

		Comparison						
Management	**Substrate**	**vs**	**Management**	**Substrate**	**Ratio**	**SE**	**z**	**$P_{bonferroni}$**
MPA	HC	-	NPA	HC	2.58	0.07	33.37	<.001
MPA	MA	-	NPA	MA	0.26	0.01	-35.19	<.001
MPA	RUB	-	NPA	RUB	1.08	0.03	2.79	0.147
MPA	SC	-	NPA	SC	2.53	0.13	18.18	<.001

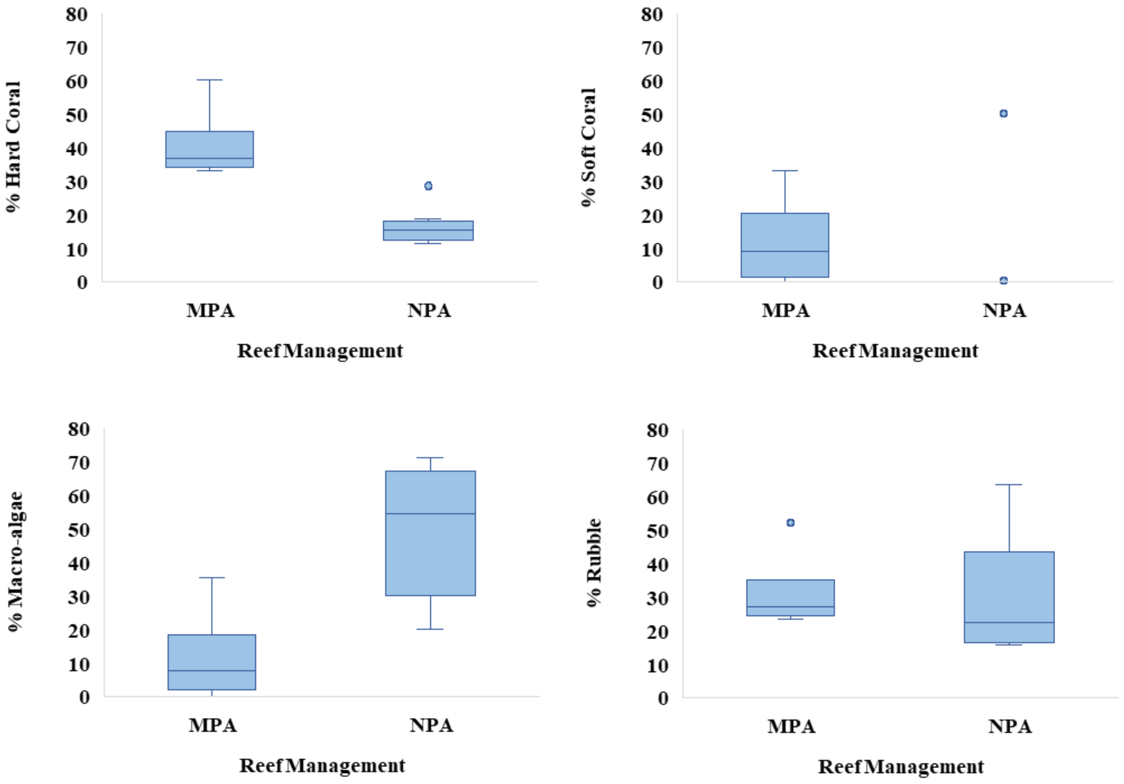

Figure 2. The difference in % substrate cover between MPAs and NPA sites surveyed around Rodrigues Island, Republic of Mauritius

Occurrence and distribution of corals in Rodrigues

Overall, 150 coral species were inventoried from the 14 sites surveyed, which included the targeted 9 rare and regionally endemic coral species from 38 genera and an addition of 2 coral species, one from the genus Acropora and one from Stylophora, which could not be identified. Furthermore, the results showed that 32 coral species occurred in relatively low numbers of colonies (n<3) within one or two surveyed sites, while 27 different coral species, which are geographically limited to the Pacific Ocean, were also found to occur at some studied sites in Rodrigues (Table 4). The MPAs had harbored the most coral genera ranging between 12 and 17 with mean occurrence of 14.25±1.11 (± S.E.) coral genera per site, which significantly differed from that of the NPAs which had a mean occurrence of 9.20±1.30 coral genera per site, one-way ANOVA, Welch's Test, p=0.014 (Figure 3 and Table 4, respectively). The no-take MPA, Trou Blanc, harbored 15 coral genera, while the multiple-use MPA, Vas Brulee, had 17 coral genera, whereas only one known coral genus, *Acropora*, was registered at Baie aux Huitres, contrary to La Ferme (NPA), where 15 coral genera were recorded, which included *Acropora*, *Montipora, Porites,* and *Anacropora* amongst others.

Of the 47 coral species, 20 *Acropora* species were recorded at Trou Blanc, which also included one Astreopora, one Cyphastrea, one Favia, one Favites, six Fungia, one Lithophyllon, eight Montipora, two Pavona, three Platygyra, five Pocillopora, and three *Porites* species. *Seriatopora*, *Stylophora, Symphyllia,* and *Turbinaria* occurred mainly at Anse aux Anglais, Terre Rouge, Gros Pot, and La Butte were found in low numbers of colonies (<3) sparsely distributed at the surveyed sites. Foliose and encrusting *Montipora* occurred in almost all surveyed sites, dominant at Anse aux Anglais, with all eight different species recorded, with the exception of Baie aux Huitre, Bar Chirurgien, and Grand Baie. Moreover, *Gardineroseris planulata*, *Hydnophora exesa*, *Oxypora lacera*, and *Plesiastrea versipora* were uniquely found at Gros Pot (NPA), whereas *Heliopora coerulea* was observed at Trou Blanc and Vas Brulee (MPAs). The common coral *Galaxea* and the endemic *A. rodriguensis* were hardly observed at the surveyed sites.

Coral species dominance in MPAs v/s NPAs (fishing zones)

Trou Blanc, the no-take MPA was the most dominant in coral species of all surveyed sites with 47 coral species of which 20 were from *Acropora* genus followed by Anse aux Anglais (MPA- Multiple use zones) with 16 *Acropora* species from 39 total coral species registered while Riviere Banane (MPA- Multiple use zone) had only two *Acropora* species from a total of 18 coral species recorded. La Ferme, Bar Chirurgien, and Gros Pot had the most coral genera and species of all the NPAs surveyed, while Baie aux Huitres had the lowest coral genera with only eight coral species from two genera, of which seven were *Acropora* spp. Moreover, 13 coral genera were recorded at Trou Mullet II (NPA) with 18 coral species, which included two Acropora species. Likewise, La Pass La Butte had seven coral genera with three Acropora spp. of a total of nine coral species recorded. It was further observed that the fishing activities had a significant impact on both coral genera and Acropora diversity within the NPAs, while hardly any such differences were found between no-take and multi-use zones MPAs (Table 5).

Table 4. Comparison of coral genera diversity between MPAs and NPAs, One-way ANOVA-Welch's Test, p<0.005, Shapiro-Wilk Test for normality, p>0.05

	F	df1	df2	p
Coral Genera MPA v/s NPA	8.75	1	10.37	0.014

Table 5. Comparison of coral species diversity in no-take and multi-use MPAs and areas subject to fishing activities, i.e., the NPAs, ANOVA, Post-hoc Tukey Test, p<0.05

	ANOVA - Coral spp.			
Sum of squares	**df**	**Mean square**	**F**	**p**
Activities	1206.76	2	603.38	8.13
Residuals	816.67	11	74.24	

Post Hoc Tukey comparisons - activities

Activities	Mean difference	SE	df	t	P Tukey
Fishing - Multi-Use	-16.33	5.67	11.00	-2.88	0.037
Fishing - No-Take	-29.00	9.04	11.00	-3.21	0.021
Multi-Use - No-Take	-12.67	9.95	11.00	-1.27	0.438

Note: Comparisons are based on estimated marginal means

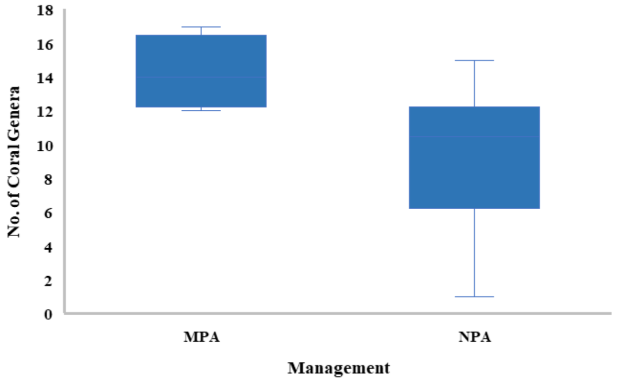

Figure 3. The difference in coral genera between MPAs and NPAs, and between MPA and NPA sites

Coral diversity indices in Rodrigues

The *Acropora* genus was the most dominant in the MPAs, followed by *Montipora*, *Favia*, *Porites*, *Pocillopora*, *Platygyra*, and *Pavona*, while *Anacropora*, *Astreopora*, *Cyphastrea*, *Echinopora*, *Favites*, *Goniopora*, *Leptatsria*, *Leptoria*, *Lobophyllia*, *Seriatopora*, and *Stylophora* were mainly observed in the NPAs, with limited *Acropora* and *Montipora* species. The reef of the no-take MPA, Trou Blanc, had a moderate genus richness (Shannon Index, H=1.67) with 15 coral genera and 47 coral species, of which 20 were *Acropora* and 7 *Montipora* species, including non-*Acropora* species evenly distributed (Pielou's Evenness, J=0.65) as compared to any other study sites (Table 6). The dominance of certain corals were considerable in the multiple-use MPAs and NPAs whereby some coral genera mainly the foliose, encrusting and massive ones were comparatively higher in densities, for instance, the highest level of coral genera richness occurred at Riviere Banane, La Ferme, Trou Mullet II and Terre Rouge (H'=2.41, 2.15, 2.14, and 2.13, respectively) with the Pielou's Evenness Index, J<0.16, indicating uneven genera distribution with potential high rarity rate against Trou Blanc (H'=1.67; J=0.65). For the rest of the sites, the H-value varied between 1.71 and 1.82, with the exception of Trou Mullet I, where the genera were relatively the lowest, H' = 0.92, with four coral genera and 12 coral species, of which eight corals were from the genus *Acropora*.

The highest level of coral genera occurred at Riviere Banane, La Ferme, Trou Mullet II, and Terre Rouge (H'=2.41, 2.15, 2.14, and 2.13, respectively) as compared to Vas Brulee (H'=1.99) and Trou Blanc (H'=1.67). For the rest of the sites, the H-value varied between 1.71 and 1.82, with the exception of Trou Mullet I, where only four genera were recorded, H'=0.92, which included 12 coral species, of which eight corals were from the genus *Acropora*. Thus, the multiple-use MPAs Riviere Banane harbored the most diverse coral genera, followed by Vas Brulee, and Anse aux Anglais, with more varying coral forms such as encrusting and foliose *Montipora*, submassive *Pocillopora*, branching *Seriatopora*, encrusting and massive *Favia*, *Favites*, amongst others, J=0.96; 0.70; 0.65, respectively. Similar results were displayed in the NPAs, whereby the various coral genera were evenly distributed at La Butte, Trou Mullet II, Terre Rouge, Grand Baie, Cavern Provert, and Bar Chirurgien (0.94<J<0.83), with over 10 coral genera per site, with the exception of Trou Mullet I. Overall, Trou Blanc displayed remarkable dominance of *Acropora* species over non-*Acropora* species as compared to NPAs, which favored relatively homogeneous low abundance non-*Acropora* species with low density of tabular *Acropora* and encrusting *Montipora*.

Occurrences and distribution of targeted endemic and rare coral species

No *A. rodriguensis*, and *Hoastrea indica*, the endemic and targeted rare coral species, respectively, were observed at the 14 surveyed sites (Figure 4). *Acropora branchi* and *P. indiania*, the two regionally endemic corals, occurred at all the surveyed MPAs when compared to NPAs. *Pocillopora indiania* was limited to Terre Rouge, while *A. branchi* further extended to Trou Mullet I and II, Gros Pot, Baie aux Huitre, and Cavern Provert in colony numbers (n<7, per site). *Acropora clathrata*, another targeted branching coral, was found to be limited to three MPA and one NPA sites, with colony numbers per site varying between n=3 to 9. *Seriatopora hystrix*, the targeted rare coral species, was only found at bar Chirurgien (n=14) and La Ferme (n=6) in limited abundance (n<3 per site); likewise, *Seriatopora caliendrium* was observed at Riviere Banane and Terre Rouge in low density (n<5). On the contrary, the targeted rare species *S. pistillata* was recorded at Anse aux Anglais, Terre Rouge, Gros Pot, La Butte, and Trou Mullet II with relatively higher colony numbers than the *Seriatopora* spp. (Figure 4).

Occurrences and distribution of targeted endemic and rare reef fishes

The endemic reef fish, *P. rodriguensis*, was observed at only one MPA surveyed site, Anse aux Anglais, while it occurred mostly in the NPAs at Trou Mullets, La Butte, La Ferme Baire aux Huitre, Terre Rouge, Cavern Provert, and Grand Baie. The other targeted regionally endemic and rare reef fishes, *Stegastes pelicieri*, *Stegastes limbatus, P. pikei*, *A. latifasciatus*, and *A. chrysogaster* were sporadically recorded in the NPA sites, contrary to *Abudeduf margariteus* and *Zebrosoma gemmatum,* which were not observed at any of the 14 surveyed sites. The Mauritian endemic fish, *S. pelicieri*, Mauritian Gregory, and *S. limbatus*, rare reef fish, were recorded in three of the surveyed MPAs, with the exception of Riviere Banane, as well as five and six MPAs respectively with numbers of individuals less than 10 (n<10), while only *S. pelicieri* was relatively numerous (n=12) in Trou Blanc (MPA): the Mauritian anemone-fish, *A. chrysogaster,* a specialized fish, limited to residing mainly in the anemone, *Heteractis magnifica,* was only observed in Trou Blanc, Vas Brulee, and Riviere Banane in areas where the anemone was present, whereas the Madagascar anemonefish, *A. latifasciatus,* mainly harboring both anemones, *Stichodactyla mertensii* and *H. magnifica,* was hardly observed in the surveyed areas (Figure 5).

Table 6. Interpretation of diversity indices to illustrate the site-wise coral species richness, the degree of variation in species using Shannon-Wiener (H) and Pielou's Evenness Index (J), indicating the diversity of coral species along with Simpson Dominance Index, D, within the surveyed MPAs and NPAs

Sites	**Shannon Index (H)**	**Simpson Diversity (D)**	**Pielou's Evenness (J)**	**Site-wise coral diversity**
Trou Blanc (No-Take MPA)	1.67	0.31	0.65	Moderate diversity with relatively fair distribution of different coral genera within the community. 47 coral spp. from 15 genera, of which 20 were *Acropora* and 7 *Montipora* spp. while others were non-*Acropora* species, which included *Favia, Porites, Pocillopora, Platygyra, and Pavona,* were observed within the no-take MPA while the reef community was dominated by *Acropora* spp.
Vas Brulee (Multiple-Use MPA)	1.99	0.71	0.21	Relatively high diversity comprising 17 coral genera with disproportionate dominance of *Acropora* and *Montipora* species, along with the new records of rare coral species, for instance, *Favia helianthoides, Pocillopora meandrina,* and *P. compressa,* were also present in low abundance.
Riviere Bananes (Multiple-Use MPA)	2.41	0.94	0.10	High coral diversity with high dominance of some non-*Acropora* genera unevenly distributed, composing mainly of *Echinopora, Favia, Fungi, Lobophyllia, Montipora, Pocillopora,* and *Seriatopora,* whereas only 2 *Acropora* species were observed
Anse aux Anglais (Multiple-Use MPA)	1.55	0.65	0.32	Moderate diversity richness with 11 coral genera dominated mainly by 16 *Acropora* spp., with uneven distributions of *Favites, Fungia, Leptoria, Pavona, Platygyra,* and certain newly recorded, rare corals such as *Acanthastrea ishigakiensis, Acropora rufus, Acropora seriata,* and *Montipora hodgsoni*
Trou Mullet I (NPA)	0.92	0.66	0.53	Low coral genus diversity with only four coral genera, whereby 8 *Acropora* spp., one *Alveopora* sp., two *Fungia* spp., and three *Porites* spp. were moderately distributed within the reef community, which also included rare *Acropora cuneata* and *A. pinguis*
Trou Mullet II (NPA)	2.14	0.89	0.14	High diversity but uneven distribution of corals with high dominance of certain corals, such as *Pavona* and *Porites.* Overall, 18 coral species from 13 coral genera were recorded, of which only three *Acropora* spp. were observed, whereas uncommon corals such as *Hydnophora excesa, Madracis kirbyi, Oxypora lacera, Pachyseris* sp., and *Stylophora pistillata* were also observed.
Bar Chirurgien (NPA)	1.99	0.22	0.83	Relatively high coral diversity and genera fairly distributed within the reef, with 25 coral species from 12 genera, consisting of 7 *Acropora* spp., including the non-*Acropora* species and an uncommon *Acropora polystoma*.
Gros Pot (NPA)	1.82	0.79	0.22	Relatively high coral diversity with the dominance of 13 *Acropora* spp. from 11 coral genera, including *Anacropora, Cyphastrea, Favia, Fungia, Gardineroseris, Leptastrea, Oullophyllia, Platygyra, Porites,* and *Stylophora*
La Pass La Butte (NPA)	1.86	0.96	0.17	Relatively high diversity with high dominance of non-*Acropora* spp. unevenly distributed amongst the seven coral genera, namely, *Acropora, Cyphastrea, Echinopora, Favites, Goniastrea, Seriatopora,* and *Stylophora*
La Ferme (NPA)	2.15	0.81	0.15	High coral genus diversity with 14 coral genera, namely, *Acropora*, *Cyphastrea*, *Echinopora*, *Gardineroseris*, *Goniastrea*, *Montipora*, *Pavona*, *Platygyra*, *Plesiastrea*, *Pocillopora*, *Porites*, *Seriatopora*, *Stylophoran*, and *Turbnarea*, including 11 *Acropora* spp. unevenly distributed
Terre Rouge (NPA)	2.13	0.89	0.12	High diversity of coral genera dominated by non-*Acropora* spp. disproportionately distributed, consisting mainly of *Cysphastrea, Favia, Montastrea, Montipora, Platygyra, Pocillopora, Seriatopora, Stylophora,* and *Turbinaria*
Cavern Provert (NPA)	1.90	0.86	0.18	Relatively high coral diversity is disproportionately distributed, consisting of *Acropora*, *Acanthastrea*, *Cyphastrea*, *Leptastrea*, *Montipora*, *Platygyra*, *Pocillopora*, *Porites*, and *Symphyllia* genera
Grand Baie (NPA)	1.70	0.87	0.22	Moderate coral diversity with seven coral genera, including *Acropora*, *Acanthastrea*, *Cyphastrea*, *Favites*, *Montipora*, *Platygyra*, and *Porites*, unevenly distributed within the reefs
Baie aux Huitres (NPA)	0	0	1.0	Only one genus, *Acropora,* consisting of eight *Acropora* spp. evenly distributed

Note: Uncommon coral indicates coral species newly recorded in the Indian Ocean as per Veron (2000) and World Register for Marine Species (WoRMS 2024)

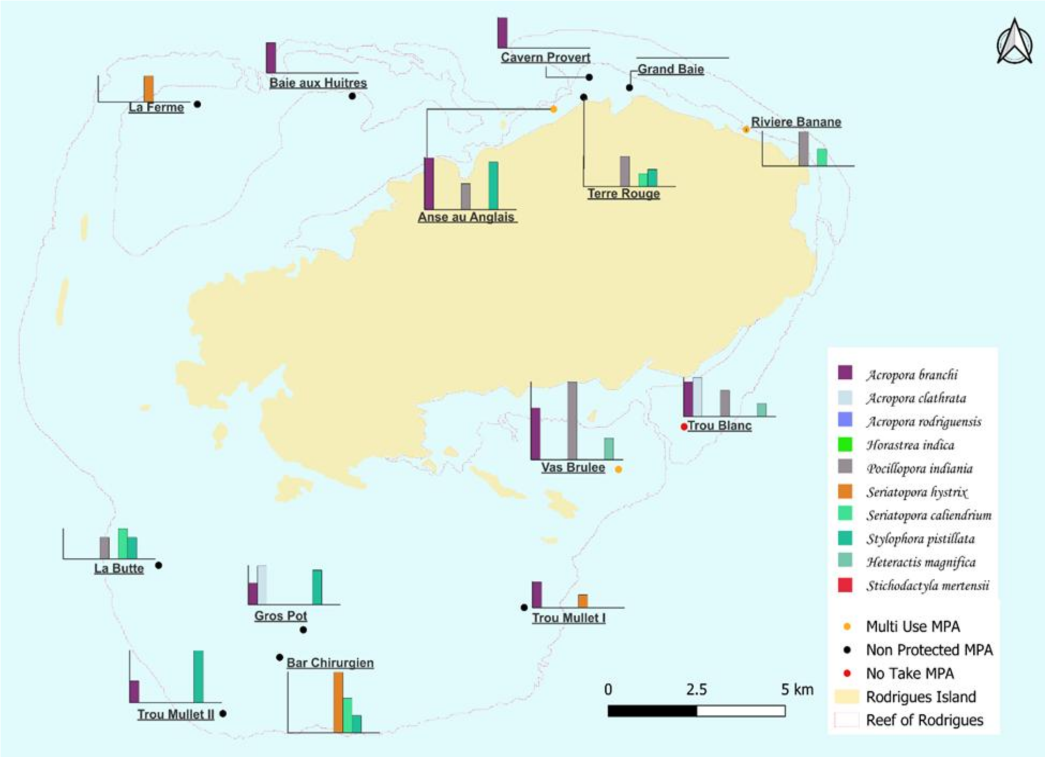

Figure 4. The geo-referenced color-coded map illustrates the occurrence of targeted rare and endemic corals recorded at the 14 surveyed sites around Rodrigues Island, Mauritius. The histograms show the occurrence of the targeted corals under the study and their relative no. of colonies with respect to other target corals, for example, only *Seriatopora hystrix* was observed at La Ferme, whereas at Grand Baie, no targeted species were observed. Likewise, no *Acropora rodriguensis* and *Hoastrea indica* were observed at the 14 surveyed sites. Note: Geo-referenced map indicates the location of each site as per the respective GPS coordinates recorded during the surveys

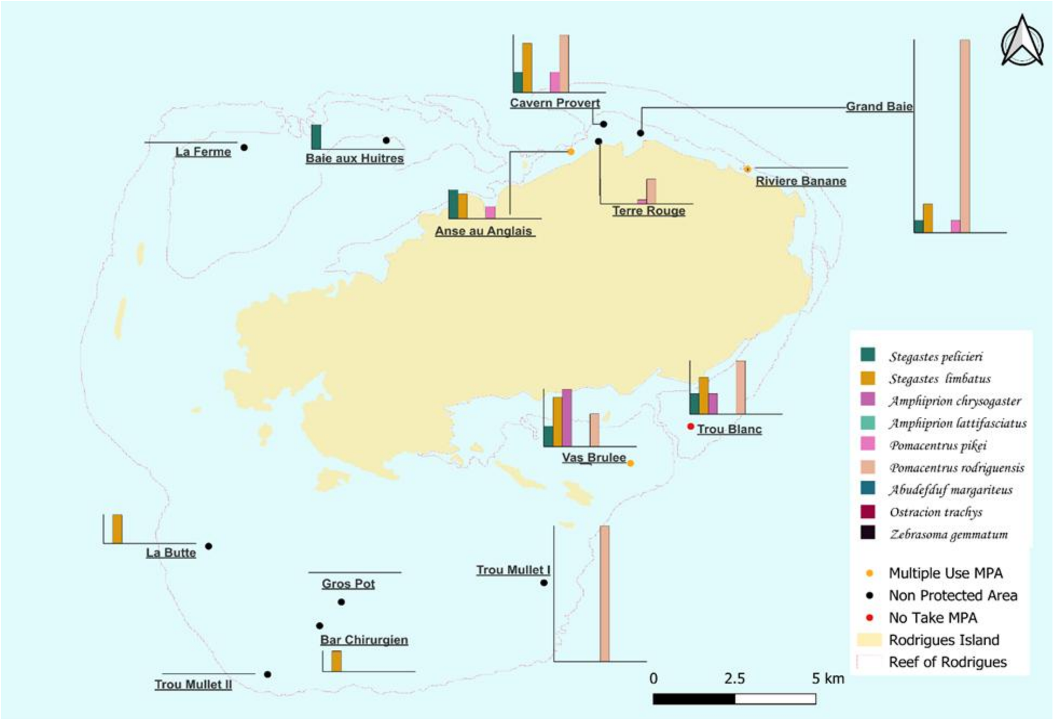

Figure 5. The geo-referenced color-coded map illustrates the occurrence of targeted rare and endemic reef fishes recorded at the 14 surveyed sites around Rodrigues Island, Mauritius. The histograms show the occurrence of the targeted reef fish species under the study and their relative density with respect to other target reef fishes within their respective site. For example, only *Pomacentrus rodriguensis* was observed at Trou Mullet I, whereas at La Ferme, Gros Pot, Trou Mullet II, and Riviere Banane, no targeted reef fish species were observed

Discussion

Coral reefs of the MPAs and NPAs in Rodrigues

This island-wide, extensive, and extended study around Rodrigues provides an in-depth insight into the status of the coral reefs within the data-limited protected and understudied non-protected areas, emphasizing targeted endemic and rare corals and reef fishes with a major focus on the implications of coral diversity and coverage both in MPAs and NPAs. This study further underpins the 3-dimensional structural functionality of the reefs with respect to the no-take marine reserve in comparison to the multiple-use MPAs and NPAs. Of the 14 sites, the no-take MPA, Trou Blanc, had the highest coral cover, dominated by the *Acropora* genus with 20 *Acropora* species along with 27 other coral species from 15 coral genera. Although 150 coral species were identified during the study, the endemic coral, *A. rodriguensis*, and the common coral *Galaxea* were hardly observed at the 14 surveyed sites, while the endemic reef fish *P. rodriguensis* was mainly found in the algal-dominated NPAs. Moreover, corals were more diverse and widely distributed in MPAs, with the dominance of the branching *Acropora* and *Montipora*, contrary to the dominance of massive, sub-massive, foliose, and encrusting corals despite low coverage in the NPAs, such as *Porites, Pocillopora, Pavona,* and *Montipora* species. Overall, the MPAs harbored the highest live coral, while the NPAs had lower live coral cover with lesser coral species diversity in algal-dominated reefs in algal and rubble-dominated reefs. It is noteworthy, the reefs of Rodrigues have been subject to continuous coastal development due to increasing population and tourists, causing mounting pressures from fisheries exploitation (Hardman et al. 2009).

MPAs v/s NPAs

Though there has been inadequate monitoring of thermal-driven coral bleaching, the fact remained that the no-take MPA, multi-use MPAs, and NPAs of Rodrigues are all exposed to the same SST warming trend with the SST anomaly fast-reaching +1.5°C (Werner et al. 2025), whereas the reefs exposed to fishing activities were the most degraded, while the multiple-use MPAs provided a limited buffer against intense fishing activities, especially during the closed season for seine netting and octopus fishery (Pasnin et al. 2018). Pasnin et al. (2018) further highlighted that the fishing activities in the Marine Reserves, for instance, octopus fishing with a harpoon, which involves trampling on the reefs, the use of a basket along with a seine net, caused serious damage to the reefs, resulting in higher rubble density both in the multiple-use MPAs and NPAs. Evidently, the reefs in the open access, NPAs exhibited extensive macroalgal coverage, especially in larger lagoons in the western region, such as Bar Chirurgien, Gros Pot, and La Butte, including the lagoons in the north at Grand Baie and Baie aux Huitres, whereas Trou Mullet I, Terre Rouge, and La Ferme had comparatively higher densities of rubbles.

The dominance of macroalgae in those mid-lagoons might be explained by the fact that larger lagoons sustained longer nutrient-rich seawater residence time due to inadequate water exchange from the ocean on account of the lack of natural passes (openings) to allow oceanic mixing (Safaie et al. 2018). The impact of the reef degradation was evident, which was depicted by high rubble coverages within the reef of Riviere Banane and Anse aux Anglais, combined with macroalgae, yet the coral cover was relatively higher at Anse aux Anglais. On the contrary, the multiple-use MPA, Vas Brulee, had the third highest coral cover with the second lowest macroalgal coverage, and half of the coral cover as compared to Trou Blanc, the strict conservation no-take MPA. These findings therefore demonstrate that strictly conserved zones, no-take MPAs effectively conserved and protected both coral cover and coral diversity (Strain et al. 2019), conversely to reefs exposed to ongoing impacts of human activities interfering with the coastal ecosystems in the multiple-use MPAs and NPAs, mainly dominated by macroalgae and rubbles (Hein et al. 2015; Cartwright et al. 2023).

On the contrary, higher coral cover with high coral diversity was observed in the backreef of the relatively smaller lagoons closer to natural reef openings. Furthermore, with a mean annual precipitation of 1,348 mm (150Mm^3/year) over an area of about 110 km^2, mountainous landmass of Rodrigues, (Ministry of Public Utilities 2008) and a predominantly north-westerly wind-driven surface current ranging between <0.1 to <0.5 m/s in the lagoon, the reefs are continuously exposed to runoffs and mass sedimentation leading to eutrophication and macroalgal proliferation (Rees et al. 2005). Conversely, the two MPAs, Trou Blanc and Vas Brulee, had the lowest macroalgal proliferation. In addition to high coral cover, the two MPAs also harbored rarely occurring soft corals at relatively higher coverage. In contrast, Trou Mullet I (NPA) had the highest soft corals of the studied sites. Unlike hard corals, soft corals were previously considered a poor habitat due to their biochemical defence mechanisms and lack of structural complexity (Dinesen 1983; Norström et al. 2009). However, recent studies have revealed that soft corals are capable of supporting diverse reef fishes in higher density (Pratchett 2005; Ferrari 2017; Epstein and Kingsford 2019), which was noticeable in Trou Blanc and Vas Brulee.

Endemic and rare species

No *A. rodriguensis*, the endemic coral of Rodrigues, was observed at the 14 surveyed sites, whereas Pasnin et al. (2018) noted the occurrence in low density at Anse aux Anglais, a common study site. During the field surveys and communication with the fishermen community and dive centers in Rodrigues, most participants associated Riviere Banane (multi-use MPA) with *A. rodriguensis*, yet despite intensive and extended coral search activities, no *A. rodriguensis* was observed; instead, only one *Acropora* species, namely, *A. irregularis,* was recorded over two one-hour coral searches. *In situ*, the dive instructor showed plate-like corals most likely to be an *Echinopora* species as the *A. rodriguensis*, which was common at the study site. No morphologically comparative study could be carried out as the literature search was limited to Fenner et al. (2004) and Pasnin et al. (2018), which only mentioned the occurrence of *A. rodriguensis* without any coral morphological description, color, or habitat or abundance status. Further online search on the endemic coral species from the World Register of Marine Species (WORMS 2024), and Corals of the World (Veron et al. 2016) resulted in no data. Under such circumstances, it is ecologically critical that genetic studies be carried out to eliminate any scientific misidentification of such corals.

The findings of this study support the observation of Obura (2016), who has indicated that the regionally endemic *A. branchi* and *P. indiania* occurred widely in the Indian Ocean, while no observation of these two corals in Rodrigues was made by either Fenner et al. (2004) or Pasnin et al. (2018). However, the current findings have demonstrated that the occurrence of both corals extended eastward of the Indian Ocean within the reefs of Rodrigues. Moreover, despite ongoing repetitive thermal stresses (Zinke et al. 2018) and vulnerability to fishing activities (Pasnin et al. 2018), both the MPAs and the NPAs harbored the regionally *A. branchi* while *P. indiana* was recorded in all MPAs, but was limited to Terre Rouge (NPA) only. Similar observation was made for another targeted rare tabular coral, *A. clathrata*, which was limited to MPAs, with the exception of only one NPA.

Moreover, the rare *S. hystrix* was relatively dominant at Bar Chirurgien (NPA), a reef dominated by macroalgae with only 12% live coral, which might potentially be explained by the fact that *S. histrix* finds its resilience under the shade (low-light) of the macroalgal mat against thermal stresses (Lewis and Altieri 2025), which also aligns with the observation made on the occurrence of *S. histrix* in an algal-dominant reef at Bamboux Virieux in Mauritius (Munbodhe et al. 2023). Furthermore, the thermal stress experiment (Munbodhe et al. 2023) showed that *S. histrix* had a comparatively higher thermal threshold than A. *branchi* and *P. indiania*, although the low colony numbers might be explained by the fact that algal-overgrowth outcompetes the expansion of these corals. Of the 14 surveyed sites, *S. caliendrium* was limited to low density at only two sites, Riviere Banane (MPA) and Terre Rouge (NPA). Under the current situation, should *S. caliendrium* be unable to acclimate to the ongoing thermal stresses, in the long run, there exists a potential threat that the latter might undergo extirpation (McClanahan et al. 2021).

Conversely, *S. pistillata* had an extended occurrence both at Riviere Banane (MPA) and three NPAs in greater densities as compared to *S. histrix*, thus showing better adaptation to algal-dominated reefs, conversely to *H. indica*, which was not observed at all at the 14 surveyed sites. Overall, the MPAs harbored both the regionally endemic corals along with other coral species, providing protection and efficiently conserving higher coral diversity, in particular, the no-take MPA, which remained an instrumental tool for conservation.

The Rodriguan endemic reef fish, *P. rodriguensis,* was abundantly found in the NPAs and at only one MPA, Riviere Banane. *Pomacentrus rodriguensis* was evidently dominant in high densities (n>100) in algal-dominated reefs of the NPAs and the one MPA, indicating that the preferred habitat for *P. rodriguensis* was the algal mats. The Mauritian endemic reef fish *S. pelicieri* and the Mauritian clownfish *A. chrysogaster* were also found for the first time in the waters of Rodrigues, more precisely in the non-protected reefs of Rodrigues, with the exception that *S. pelicieri* was also observed at Riviere Banane (MPA). The occurrence of both fish species endemic to Mauritius in the reefs of Rodrigues suggests that the range of these endemics expands further to the East of the Mascarene Plateau, thereby signifying wider dispersal capabilities, which warrant dispersal and connectivity studies for potential extension within the different islands of the Indian Ocean. Similarly, the targeted rare reef fishes, *S. limbatus* and *P. pikei,* were mostly observed at some NPA sites in low densities, whereas the Madagascar anemonefish *A. latifasciatus*, *A. margariteus,* and *Z. gemmatum* were hardly encountered at any of the 14 surveyed sites, which need further in-depth investigation for better clarity on the occurrence and distribution of these species within the Mascarene Plateau.

Coral diversity richness

Of the 14 sites surveyed, 150 coral species were recorded from 38 genera, while 47 species belonged to the genus Acropora, which mainly occurred in the MPAs, with the exception of Riviere Bananes, where only two *Acropora* species were observed. These detailed observations supplement the last coral inventory for Rodrigues, which dates back to 2004, whereby 130 coral species from 40 coral genera were recorded from 26 inside and off-lagoon sites, inclusive (Fenner et al. 2004). As such, the dominance of branching and submassive *Acropora* indicated the reef structural complexities in the MPAs, while the low *Acropora* diversity along with high macroalgal and rubble cover was significantly reflected in the NPAs (Hardman et al. 2009). Similar observations were also made by Pasnin et al. (2018), who summarized 14 *Acropora* species from Riviere Bananes, Anse aux Anglais, Grand Bassin, and Passe Demie multiple-use MPAs (the last two were not included in this study). It was further observed that the fishing activities had a significant impact on both coral genera and *Acropora* diversity within the NPAs, while hardly any such differences were found between no-take and multi-use zones MPAs.

Moreover, both the no-take zone and the multiple-use MPAs had most of the branching *Acropora* and encrusting *Montipora* at the studied sites. Although the coral species diversity was higher in MPAs, the NPAs harbored various branching non-*Acropora* at low coverage, such as *Pocillopora*, *Porites*, *Seriatopora*, and *Stylophora* species, along with encrusting and plate-like *Montipora,* encrusting *Astreopora*, *Cyphastrea*, *Echinopora*, *Leptoria*, *Pavona***,** and *Turbinaria*, as well as sub-massive and massive *Porites*, *Heliopora*, *Gardineroseris*, *Goniastrea*, *Goniopora*, *Oulophyllia*, *Platygyra*, and *Symphyllia*. Non-Acropora. Despite low densities, the NPAs also included uncommon and rare species, for instance, *Acanthastrea regularis*, *Montipora kellyi*, and *Porites cumulatus* were found in Grand Baie; likewise, *Anacropora forbesi* and *Cyphastrea calcidium* were recorded for the first time in

Rodrigues at Gros Pot. As such, despite being low in coral density, the NPAs supported the existence of rare non-*Acropora* branching, plate-like, and encrusting corals, which also contributed to the species diversity, mandating an ecosystem approach to fisheries for better biodiversity protection and conservation.

Future reef management strategies

This comparison between the NPAs and MPAs, therefore, essentially provides research-driven evidence that the MPAs harbored the most structurally complexed corals, high in diversity and extended to a wider area despite a challengingly warming environment at the expense of fishing areas driven by dense macroalgae and rubbles (Hardman et al. 2009; Elliott et al. 2018; McClanahan and Muthiga 2021; De et al. 2022; Doorga et al. 2025). Although this study is limited to a one-time coral reef survey around Rodrigues, it has demonstrated the crucial roles of MPAs as the main buffer against major human disturbances by maintaining the ecologically essential 3-dimensional functional reef structures while enhancing ecosystem resilience against ongoing accelerating trends in marine heating. Besides biodiversity protection and through spillover, the no-take MPA effectively provides both social and economic sustainability to the immediate coastal communities of the Small Island Developing States (SIDS). It is therefore advocated that, in addition to no-take MPAs, replications of multiple-use MPAs shall be promoted to establish effective MPA networks (Eli et al. 2025). Such initiatives shall be accompanied by the implementation of an ecosystem approach to fisheries, supported by appropriate policies including reinforced enforcement and collaborative management strategies, which in turn, may potentially mitigate the predicted decline in marine species (Hughes et al. 2017) and, in the future, reinforce the existing marine biodiversity and ensure food security within the region.

In conclusion, this multifaceted study, first of its kind in the reefs of Rodrigues, has demonstrated that intense human activities leading to irreversible degradation of reefs are causing major shifts from functionally active coral ecosystems to macroalgal and rubble-dominated reefs. In an era of prolonged marine heating, frequent and severe coral bleaching events, the study clearly demonstrated that the areas under permanent fishing pressure have been significantly impacted, provoking widespread algal growth with a major shift from live coral to rubble-dominated reef, while the strictly conserved reef remarkably sustained a high coral cover and coral diversity with negligible algal coverage. As such, the no-take MPA in Rodrigues remained instrumental in reef management by protecting the marine biodiversity. Furthermore, the study also established that all the studied MPAs effectively act as a buffer for sustaining complex coral structures, both in terms of coral coverage and diversity, and, by virtue, provide enhanced reef resilience, more specifically in the no-take marine reserve, as compared to the macroalgal and rubble-dominated MPAs.

However, the study was limited to a single survey period, lacked temporal replication, and relied on visual census methods that may overlook cryptic species. Absence of genetic and physicochemical data restricted confirmation of species identity and environmental drivers of reef change. Future work should employ long-term monitoring, molecular identification, and remote sensing to validate coral diversity and detect recovery trends. Integrating water quality, sedimentation, and socio-ecological assessments will strengthen MPA management and coral reef conservation strategies in Rodrigues. Overall, these findings align with one of the United Nations goals, SDG 14: life below water, to "conserve and sustainably use the oceans, seas and marine resources" whereby the results provide vital information on the health status of the coral reefs of Rodrigues and suggest that collaborative reef management is crucial for ecological and socio-economic sustainability. Furthermore, while complementing the critical scientific information gap on regionally endemic and rare corals and reef fishes, the study also provides critical insights into reef vulnerability due to intense fishing activities. These findings therefore suggest that reefs under protection are more resilient and that promoting an ecosystem approach to fisheries may further enhance overall reef resilience and strengthen the conservation strategies for the critical marine ecosystem and its associated biodiversity in a challengingly warming environment.

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Distribution and photo-physiology of bleached and non-bleached *Sarcophyton* sp. in Rodrigues reefs, Republic of Mauritius

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Abstract. *Ramkalam MK, Korimbocus AM, Jogee SY, Gerzer F, Nundlall Y, Chatoolsingh D, Anansamy M, Kaullysing D, Casareto BE, Suzuki Y, Reimer J, Wijayanti DP, Nascimento B, Bhagooli R. 2025. Distribution and photo-physiology of bleached and non-bleached* Sarcophyton *sp. in Rodrigues reefs, Republic of Mauritius. Indo Pac J Ocean Life 9: 156-164.* Soft corals are key contributors to reef ecosystems, especially where hard coral cover is declining, yet their responses to bleaching stress remain poorly understood in the Indian Ocean. This study investigated the distribution and abundance of soft corals, alongside the photosynthetic performance of bleached and non-bleached *Sarcophyton* sp. around Rodrigues Island, Republic of Mauritius. Field surveys were carried out using Line Intercept Transects (LIT) across four sites: Ti Trou, Plateau Benitiers, Var Brulee, and Pate Reynieux, revealing significant variations in the soft coral communities. For healthy and bleached *Sarcophyton* colonies, chlorophyll fluorescence was measured using a JUNIOR Pulse-Amplitude-Modulated (J-PAM) to assess the photo-physiology (Y(II), $rETR_{max}$, NPQ_{max}). Results showed that soft corals flourished at shallow southern sites (65.00±0.26% and 51.67±4.72%) with lower levels of nitrate and phosphate. The photo-physiological analyses showed that healthy *Sarcophyton* sp. had higher Y(II) (0.509±0.004) and $rETR_{max}$ values (15.23±4.2) compared to bleached *Sarcophyton* sp. (Y(II); 0.163±0.05, $rETR_{max}$; 0.97±0.42), while NPQ_{max} values remained similar (healthy looking; 0.09±0.02, bleached; 0.06±0.008). The retention of quenching activity suggests that even bleached the *Sarcophyton* samples still had some protective mechanisms hence the possibility of remaining symbionts. These findings demonstrate the physiological plasticity and resilience of *Sarcophyton* sp., which may contribute to adaptation and resilience to stress conditions and contributes to shifts in reef communities.

Keywords: Bleaching, chlorophyll fluorometery, coral distribution patterns, Rodrigues Island, *Sarcophyton*

Abbreviations: CF: Chlorophyll Fluorescence, DO: Dissolved oxygen, ETR: Electron transport rate, Fm: Maximal fluorescence yield of dark adapted sample with closed PSII centers, Fm': Maximal fluorescence yield of illuminated sample with closed PSII centers, HC: Hard Coral, LIT: Line intercept transect, NPQ: Non-photochemical quenching parameter, PAM: Pulse Amplitude Modulation, PB: Plateau Benitiers, PR: Pate Reynieux, PS: Maximum potential rETR, PSII: Photosystem II, rETRmax: Maximum photosynthetic capacity, RLC: Rapid light curve, SC: Soft Coral, sp.: species, TT: Ti Trou, VB: Var Brulee, WIO: Western Indian Ocean, Y(II): Effective quantum yield, Y: Quantum yield calculated through PAM, α: Photosynthetic efficiency of PSII; ascending slope of a rapid light curve, β: Photoinhibition of PSII; descending slope of a rapid light curve

INTRODUCTION

Ubiquitous in many benthic marine environments, from tropical to polar waters, from intertidal to deep waters, octocorals are sessile benthic organisms within the class Octocorallia (Cnidaria: Anthozoa) (Alderslade 1987). Unlike their hard scleractinian coral counterparts, soft corals lack a calcareous skeleton or internal axis, and instead, possess a flexible, often gelatinous body structure supported by microscopic, calcified sclerites (Hardman et al. 2007). Soft corals can settle and grow on a wide range of substrates, including coral reefs and rocky substrates, depending on the species (Chanmethakul and Chansang 2009). These filter feeders would create vibrantly coloured colonies by joining polyps together (Fabricius and Alderslade 2001; Behera et al. 2024). However, due to their diversity and morphological plasticity, soft corals are often hard to identify to species-level (Fabricius and Alderslade 2001).

Soft corals rely less on reef-building than their hard coral counterparts, though Jeng et al. (2011) demonstrated that *Sinularia* species can contribute to reef frameworks through spiculite formation. Such structures occur in various parts of the world including the south of Japan, Australia and Somalia. However, the formation and growth of colonies depend on various physical environmental factors of their habitat, such as water flow, current, depth, and turbidity (Fabricius and Klumpp 1995; Fabricius and De'ath 1997; Chanmethakul and Chansang 2009), as well as irradiance for zooxanthellate species. Their ecological success is linked to both structural and chemical strategies. In the absence of a protective skeleton, many species deploy antioxidant responses, heat-shock proteins, and secondary metabolites to defend against stress and predation (Feder and Hofmann 1999; Wah et al. 2007). These metabolites have also attracted biomedical interest, showing activities such as anti-inflammatory, antimicrobial, and anticancer effects (Zubair et al. 2015; Jahajeeah et al. 2023a, b).

Despite their ecological attributes and pharmaceutical relevance, little research has been conducted in Rodrigues Island situated in the western Indian Ocean. The existing baseline ecological and physiological data regarding Rodrigues' octocorals are extremely sparse, representing only a handful of taxonomic surveys from the late 1900s and one recent ecological assessment. Part of the Mascasrene Islands and the Republic of Mauritius, Rodrigues harbours one of the most abundant and diverse marine ecosystems. Species of soft corals were identified and reported by Tixier-Durivault (1966) and Michel (1974), including species from the genera *Alcyonium*, *Cladiella*, *Lobophytum*, *Pareythropodium*, *Sarcophyton*, *Sinularia*, *Nepthea* and *Stereonephthya*. The most recent study conducted by Jahajeeah et al. (2021) reported valuable insights on the Rodriguans soft corals, mainly their diversity and abundance around the island, with species from the genera *Sinularia, Lobophytum* and *Sarcophyton* being the most commonly observed. Other genera, such as *Cladiella, Dendronephthya* and *Heteroxenia* were also observed but in lesser numbers (Jahajeeah et al. 2021).

Similar to hard scleractinian corals, zooxanthellate soft corals also bleach and suffer other stress-related impacts when exposed to higher temperatures, fluctuating light intensities, and shifts in water quality (Michalek-Wagner and Willis 2001; Slattery et al. 2019). Zooxanthellate soft corals bleach under stress conditions due to the loss of these symbionts or their photosynthetic pigments (Suzuki et al. 2015; Casareto et al. 2016). Induced under conditions of environmental stress, such as rising sea temperatures, intense light, and salinity and nutrient changes, which affect the delicate balance of the symbiosis and cause large-scale bleaching events threatening the survival of coral reef ecosystems (Bhagooli et al. 2021, 2022). Photophysiology, therefore is a valuable tool to understand how symbiotic soft corals respond to environmental stressors such as heat, light, and salinity changes. Temperature has a significant impact on the optimal growth and photosynthetic efficiency of symbionts (Fitt et al. 2000; Mattan-Moorgawa et al. 2012, 2018; Sammarco and Strychar 2013; Bhagooli et al. 2022; Jeetun et al. 2023). Slattery et al. (2019) reported that continuous thermal stress caused a decline in resistance, resilience, and population density and increased mortality of soft corals in Guam. These coral species span a variety of environments and thus have differential responses to climate changes based on their unique adaptations. For instance, Robinson and Warner (2006) reported that differences in Symbiodiniaceae adapted to different environments can result in large differences in their photosynthetic responses to thermal stress. The dysfunction in photosynthesis is a key trigger for symbiont cell loss and eventual coral bleaching.

Studies on distributions, abundances, and photosynthetic performances of soft corals are needed to contribute to a better understanding of the ecological dynamics of coral reef ecosystems. Such studies are sparse for the waters around Rodrigues Island. Therefore, the aim of this study was to evaluate the distributions and abundances of soft corals around Rodrigues Island. Furthermore, this study also assessed the photobiology of bleached and non-bleached *Sarcophyton* sp., which was one of the widely distributed species around Rodrigues Island, to examine its physiological responses during a period of high sea surface temperatures.

MATERIALS AND METHODS

Study area

Rodrigues Island is a small volcanic island located in the southwest Indian Ocean (19°42'33"S, 63°26'33"E) and an autonomous outer island of the Republic of Mauritius. The island features a rich marine ecosystem, characterized by extensive coral reefs that are recognized as a global biodiversity hotspot. For this research, four study sites around the island, two in the north and two in the south, were selected based on preliminary visual observations and previous reports (Figure 1; Table 1) to ensure presence of soft corals.

Field surveys

Surveys were conducted using the Line Intercept Transect (LIT) method by Niamaimandi et al. (2017) during April 2024. These surveys were carried out by snorkeling and/or diving at depths ranging from 1 meter to 10 meters across four study sites around Rodrigues. At each study site, three transects of 50 meters each were laid parallel to shoreline. Data was recorded systematically at each transect, noting the length of the transect intersecting with soft coral colonies. Soft corals were identified to genus level during the survey based on their morphology, which was then verified using identification guides (Fabricius and Alderslade 2001; McFadden et al. 2025) using images taken along video transects. Genus, growth form, and intersection length (cm) were used to calculate percentage cover. Physical properties such as sea surface temperature and salinity were documented at every station (3 measurements per transects) using a thermometer and a digital refractometer (Milwakee Digital Salinity refractometer) respectively. water samples (n=3 per site) were collected to analyze nutrient concentration and stored in ice before laboratory analysis as described by Margeson et al. (1980) and Murphy and Riley (1962) (Table 1).

Chlorophyll fluorescence measurement

Photosynthetic performances of collected *Sarcophyton* sp. samples were measured using a JUNIOR Pulse Amplitude Modulation (JUNIOR-PAM, Walz GmbH, Germany) fluorometer. The JUNIOR-PAM measures the variations of Chlorophyll Fluorescence (CF) of a biological material (Schreiber et al. 1986). It consists of a 50 cm long plastic fiber which releases saturating pulses measuring the variable CF emitted by the photosystem II of living materials.

Bleached and healthy-looking tissue samples of soft coral colonies from the genus were collected at approximately 5 m water depth. Colonies were classified as ‘healthy-looking’ when exhibiting usual brown or colourful pigmentation and ‘bleached’ when displaying paling tissue paling or whitening consistent with symbiont loss. For each condition, three colonies were selected, and three tissue samples were collected from each colony. The JUNIOR-PAM fiber was placed onto the surface of both the healthy and bleached soft coral samples to measure the CF of that specific area after a minimum of 20 min dark adaptation period. A minimum of three area of interest was selected for each soft coral sample. Photosynthetic parameters including YII, $rETR_{max}$, and NPQ_{max} of the both soft coral samples were obtained using the software Wincontrol-3 (v3.36, Heinz Walz GmbH). Rapid light curves were conducted using the following actinic light intensities and/or PAR (photosynthetically active radiation at the time of measurement).; 0, 65, 90, 125, 190, 285, 420, 625, and 820 µmol photons m^{-2} s^{-1}. Each measurement was taken for about 60 seconds. Y(II), $rETR$ and NPQ was calculated as indicated.

Effective quantum yield (YII):

$Y(II) = (F_m' - F) / F'_m$

Where:

F: Fluorescence yield

F_m: Maximal fluorescence yield of sample after adaptation in dark

F_m': Maximal fluorescence yield of sample in illumination (Schreiber and Klughammer 2008)

Maximum electron transport rate ($rETR_{max}$):

$rETR = Y(II) \ x \ PAR \ x \ 0.5$ (µmol electrons m^{-2} s^{-1})

$rETR_{max} = P_{max}$ (determined from light curve)

Where:

PAR: Photosynthetically Active Radiation at the time of measurement (µmol photons m^{-2} s^{-1})

rETR: Relative electron transport rate (µmol electrons m^{-2} s^{-1})

Y(II): Effective quantum yield of photosystem II

0.5: Factor assuming equal distribution of light energy between photosystems I and II (Ralph and Gademann 2005)

Table 1. Coordinates and description of selected study sites across Rodrigues Island, Republic of Mauritius

Study sites	Coordinates	Site description			
		Protected/ Non protected	Depth	Reef type	Substrate type
Ti Trou	19.6625°S 63.4389°E	Non protected	5 - 10 m	Reef crest	Fine sediment with patches of coral rubbles
Plateau Benitiers	19.66722°S 63.43556°E	Non protected	5 - 10 m	Reef crest	Fine sediment with patches of coral rubbles
Var Bruleee	19.747722°S 63.472667°E	Protected	~ 2 m	Reef flat	Coral rubbles with patches of sand
Pate Reynieux	19.749444°S 63.468889°E	Protected	~ 2 m	Reef flat	Coral rubbles with patches of sand

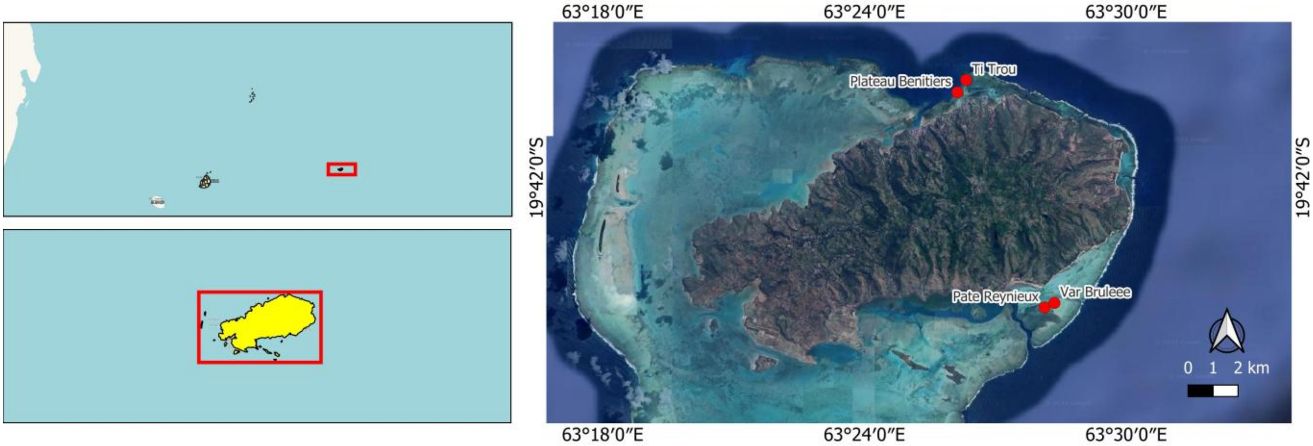

Figure 1. Map of Western Indian Ocean showing the location of Rodrigues Island (left) and Map of Rodrigues Island (Republic of Mauritius) showing locations of study sites

Non-Photochemical Quenching (NPQ):

$NPQ = (F_m - F_m') / F_m'$

Where:

F_m: Maximum fluorescence emission recorded in dark-adapted condition

F_m': Maximum fluorescence value recorded at distinct intervals of time during illumination (Klughammer and Schreiber 2008)

NPQ_{max}: Was determined from the rapid light curves

Statistical analysis

The data collected were analysed using statistical methods to determine the distribution patterns and abundance of soft corals across the surveyed sites. All analyses were carried out using IBM SPSS software. Shapiro-Wilk Test was performed to ensure normality of data and non-normal data sets were transformed using "Log10". The Shapiro-Wilk test indicated normally distributed data ($p>0.05$) for all sites and hence data was retained. Due to small sample size ($n< 15$), Kruskal-Wallis test was used to compare differences in abundances of octocorals between different sites. Spearman's rank correlation was used to examine the relationships between environmental parameters and the abundances of soft corals. While transects were nested within sites, the limited number of replicates per site restricted the possibility of mixed-effects modeling. Therefore, due to site-level differences and given the limitations on the number of transects conducted, using Kruskal-Wallis test was deemed appropriate. Kruskal-Wallis test was also used to evaluate the variation between the photosynthetic performances of both healthy and bleached *Sarcophyton* sp. tissue samples. Additionally, Spearman's rank correlation (p-value<0.05) was used to understand the difference in the photosynthetic capacity of the bleached and healthy samples.

To quantify diversity of soft corals at genus level at each site, Shanon-Wiener Index (H) was used.

Shanon Index (H) Formula:

$H=-\sum(P_i \ln P_i)$

Where:

H: Shannon Index

P_i: Proportion of individuals that belong to the th genus (relative abundance of corals)

In: Natural logarithm (Shannon and Weaver 1963)

To evaluate the dominance of soft and hard corals at genus level within groups across study sites, Simpson's Dominance Index (D) was used.

Simpson's Dominance Index Formula:

$D= \sum (P_i)^2$

Where:

D: Simpson's Dominance Index

S: Total number of genus

P_i: Proportion of individuals of the th genus (Simpson 1949)

To estimate the evenness in distribution of soft corals at genus level in the reef community, Pielou's Evenness Index (J) was used.

Pielou's Evenness Index Formula:

J = H' / In (S)

Where,

J: Pielou's Evenness Index

H': Shannon-Wiener Diversity Index

S: Total number of genus in the sample

In: Natural logarithm (Pielou 1966)

RESULTS AND DISCUSSION

Physico-chemical conditions

Temperatures recorded from all study sites, namely Ti Trou (TT), Plateau Benitiers (PB), Var Brulee (VB), and Pate Reynieux (PR), showed significant difference across study sites ($p<0.05$) (Tables 1 and 2). Depth ($p=0.028$) and chemical qualities of the seawater, particularly nitrate ($p=0.045$) concentration, showed significant disparities between the northern sites and southern sites. VB and PR had the lowest concentrations of nitrate while TT and PB had the highest (Table 1).

Benthic composition

The coral cover data from the four sites showcases significant differences in coral composition and diversity indices ($p<0.05$). Among the four survey sites, TT had relatively low soft coral covers at 3.67±2.31% (Table 3). TT and PB, showed similar profiles, with high scleractinian hard coral covers of 81.33±4.72% and 75±2.31%, respectively. Soft coral genera present in the northern sites included *Sarcophyton, Cladiella* and *Sinularia* (Figure 2). On the other hand, VB and PR had higher percentages of soft coral cover, 65.00±0.26% and 51.67±4.72%, respectively. *Heteroxenia* and *Cespithularia* were most commonly observed genera in the southern sites, where they formed large blue soft coral "carpets" in the relatively shallow waters (Figure 3). VB was observed to have the highest soft coral cover and lowest substrate cover (5±0.51%), implying very low levels of non-living substrate exposure. Substrates upon which soft corals in the southern sites grew included dead coral rubble, fine sand, and live and dead hard corals.

The Shannon-Weiner Index, a measure of soft coral diversity, was highest at PR (0.79±0.14) and at TT (0.86±0.14), indicating low to moderate diversity of soft corals compared to the other two sites which indicated moderate diversity. The dominance index for soft corals showed a higher value at PR (0.51±0.33) followed by VB (0.51±0.30) indicating that one or two soft coral genera was contributing, disproportionately, to the overall percentage cover. In contrast, the TT and PB hard coral assemblages had lower D values (~0.40) indicating a greater evenness among hard coral genera. Pielou's Evenness Index, which indicates how evenly individuals distributed among the species present, was highest at PB (0.88±0.07), hence showing that PB had a more evenly distributed soft coral distribution, with a considerable composition of hard and soft corals at 50.67±2.31% and 33.67±2.31%, respectively, followed by TT (0.81±0.30) and PR (079±0.31) (Table 3).

Photosynthetic performance

The average effective quantum yield (Y(II)) of healthy *Sarcophyton* sp. samples were observed to be significantly higher (0.509±0.004) compared to that of the bleached samples (0.163±0.05) (Figure 4). Similarly, the maximum photosynthetic activity (rETR_{max}) was found to be markedly greater ($p<0.05$) in healthy *Sarcophyton* samples (15.23±4.2) than bleached *Sarcophyton* samples (0.97±0.42). Notably, the non-photochemical quenching activity (NPQ_{max}) between the healthy samples (0.09±0.02) and the bleached samples (0.06±0.008) were not found to differ significantly (Figure 4, Table 4).

Discussion

Distribution patterns of soft corals

This study provides new evidence of the diversity and composition of soft coral assemblages around Rodrigues Island, an area where baseline ecological data remain limited. The soft coral communities encountered exhibited clear spatial heterogeneity, with the southern sites (Var Brulee and Pate Reynieux) supporting higher soft coral cover than the northern sites (Ti Trou and Plateau Benitiers). The most prevalent genera encountered in the north were *Sarcophyton*, *Cladiella*, and *Sinularia*, while *Heteroxenia* and *Cespitularia* were encountered in the south in accordance with previous assessment of Rodrigues' octocoral communities (Jahajeeah et al. 2021). Of particular interest is that the study also reports on benthic change at certain sites, with soft corals out-numbering hard corals, most particularly at Var Brulee. The observation substantiates earlier findings and suggests ongoing or incipient structural change in the reef, possibly due to synergistic natural and anthropogenic stress. While soft corals dominated total benthic cover at southern sites, their lower to moderate diversity values signify lower internal diversity but greater dominance by fewer species, which lines up with observations made whereby *Heteroxenia* and *Cespitularia* genus were the most abundant. Clear dominance by *Heteroxenia* and *Cespitularia* genera, expressed by their high percentage cover, to create extensive carpets in shallow lagoon areas is a significant feature of Rodrigues reefs not earlier well-characterized in the literature.

Ecological indices such as Shannon-Wiener diversity and Pielou's evenness also reflect differences in coral community structure among the sites. For example, Pate Reynieux had dense soft coral cover together with an uneven species distribution. The environmental conditions, in particular, nitrate and phosphate concentrations at the southern sites correlated with the higher soft coral abundance suggesting they may be associated to the nutrient-poor conditions of those areas, possibly due to the fact that hard corals are less competitive under nutrient-poor conditions, making it less competitive for the soft corals and allowing them to dominate (Baum et al. 2016). The widespread distribution of *Heteroxenia* and *Cespitularia* at the southern sites is consistent with the literature regarding these genera serving as opportunistic colonizers in shallow reef flats dominated by rubble or sand (Benayahu and Loya 1984; Fabricius and Alderslade 2001; Baum et al. 2016). Their carpet-like formations could reflect ecological release from competitive effects of scleractinians in these habitats. This study offers valuable observation data on current soft coral distribution patterns and emphasizes the need for longer duration and larger extent monitoring on Rodrigues reefs.

Table 2. Summary of Kruskal-Wallis test for the effect of depth, temperature, nitrate and phosphate among study sites

Physico-chemical conditions	df	H	P-value
Depth	3	10.913	0.012*
Temperature	3	10.913	0.012*
Nitrate	3	9.925	0.018*
Phosphate	3	7.814	0.051^{NS}

Note: *: $p<0.05$, NS: Not Significant

Table 3. Environmental parameters around study sites in Rodrigues (Mean ± SD)

Sites	Physico-chemical conditions				
	Depth (m)	Water current	Temperature (°C)	Nitrate (µmol/L)	Phosphate (µmol/L)
Ti Trou (TT)	10.70	Strong	30.0	0.04±0.001	0.09±0.01
Plateau Benitiers (PB)	11.40	Strong	30.0	0.57±0.30	0.28±0.01
Var Brulee (VB)	2.00	Low	29.5	0.003±0.001	0.03±0.001
Pate Reynieux (PR)	2.00	Low	30.0	0.01±0.02	0.03±0.01

Table 4. Coral cover and ecological indices at the four study sites around Rodrigues Island, Mauritius

Sites	Live benthic cover		Ecological indices		
	Soft coral (%)	Hard coral (%)	Shannon-Weiner Index	Simpson's Dominance Index (SC)	Pielou's Evenness Index
TT	3.67±2.31	81.33±4.72	0.64±0.12	0.43±0.001	0.81±0.30
PB	33.67±2.31	50.67±2.31	0.65±0.15	0.42±0.001	0.88±0.07
VB	65.00±0.26	30.00±6.47	0.86±0.14	0.51±0.30	0.78±0.16
PR	51.67±4.72	41.33±5.28	0.79±0.14	0.51±0.33	0.79±0.31

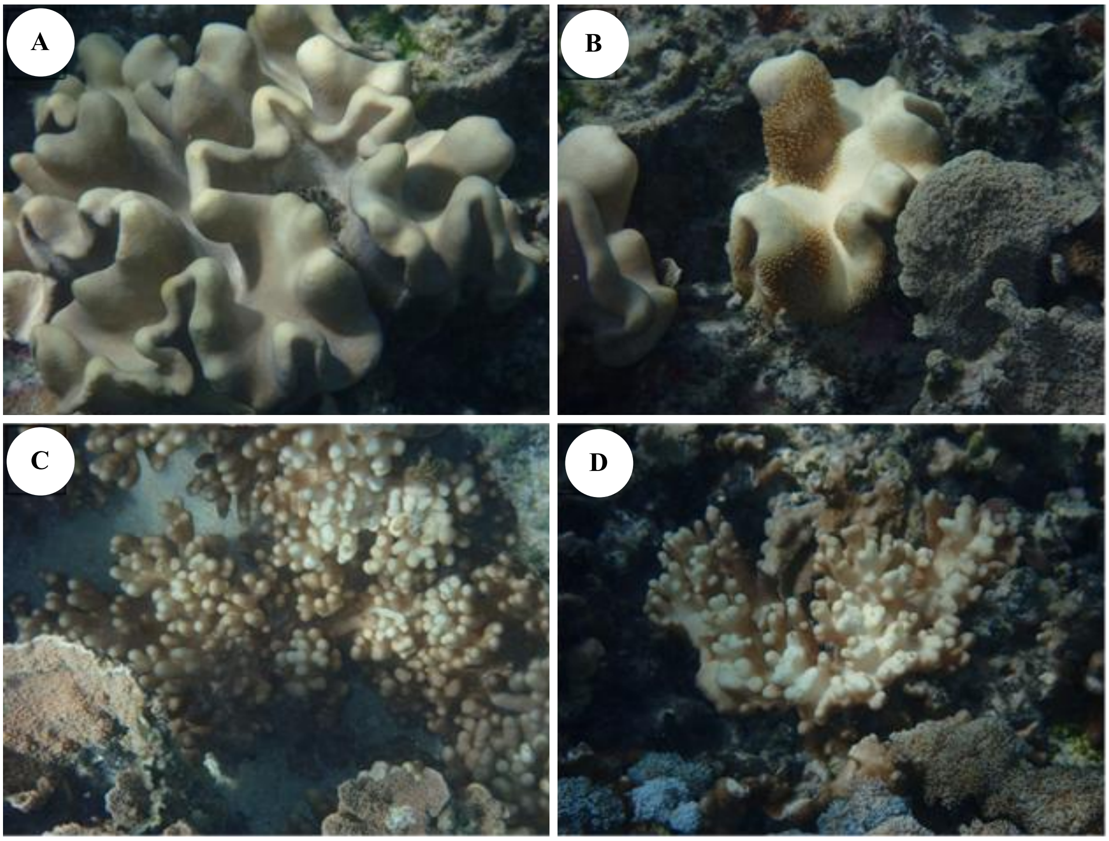

Figure 2. Corals at Ti Trou, Rodrigues Island, Mauritius. A and B. Bleached *Sarcophyton*, C and D. Partly bleached *Cladiella* at Ti Trou

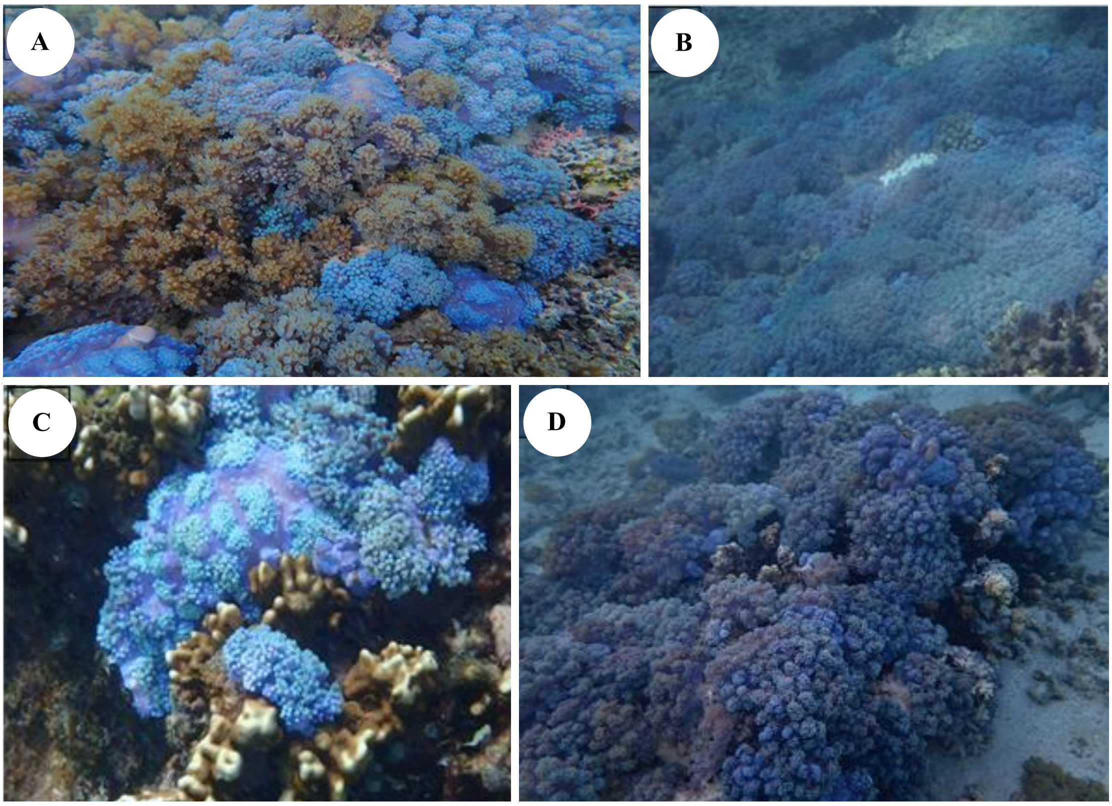

Figure 3. Corals in the Southern sites of Rodrigues Island, Mauritius. A. *Heteroxenia* sp. and *Cespithularia* sp., B. "Blue Soft Coral Carpet", C and D. Blue soft coral growing on top of hard corals

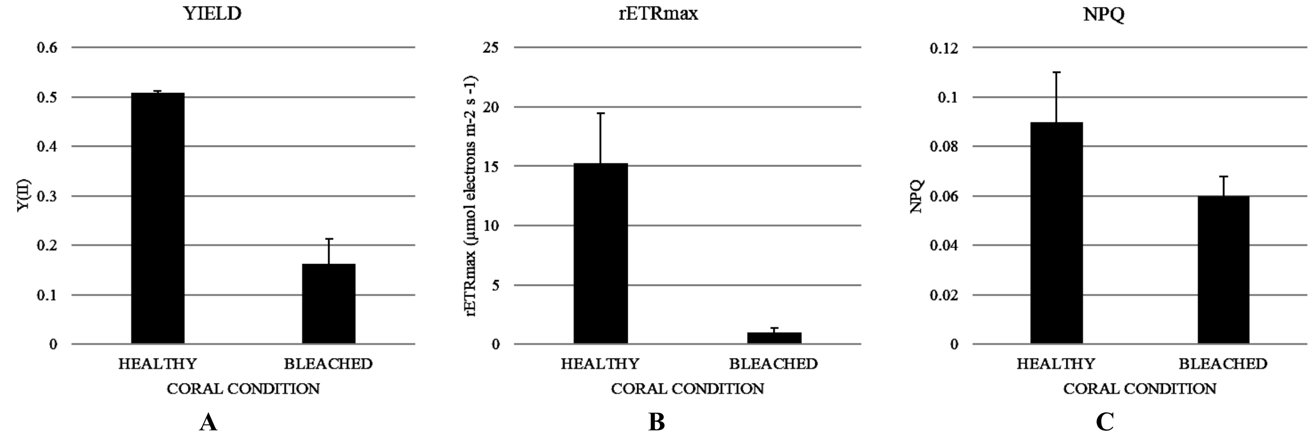

Figure 2. Photo-physiology of Bleached and Non-bleached *Sarcophyton* sp. samples. A. Quantum yield, B. rETRmax and C. NPQmax

Table 5. Kruskal-Wallis test to test effect of healthy-looking (non-bleached) and bleached conditions in *Sarcophyton* sp. on quantum yield (Y(II)), relative maximum electron transport rate (rETRmax) and non-photochemical quenching (NPQmax)

Photosynthetic parameters	df	H	P-value
Y(II)	1	7.507	0.01**
$rETR_{max}$	1	9.530	0.00**
NPQ_{max}	1	0.940	0.487^{NS}

Note: **: Significant difference at $p < 0.01$, NS: Not Significant

Photophysiology of Sarcophyton

Extreme levels of heat, light, and other environmental parameters have long been recognized to be among the main causes of bleaching events among zooxanthellate anthozoan species. Observations made during this study highlight significant distinctions between the photosynthetic apparatus of the healthy and bleached *Sarcophyton* sp. colonies. The physiological adaptability of soft corals is a key factor in their distribution and ecological success (Rocha et al. 2013; Dummee et al. 2023). The significantly higher effective quantum yield (Y(II)) and maximum photosynthetic activity ($rETR_{max}$) pointed towards the adequate efficiency of PSII photochemistry and overall good metabolic health in the healthy *Sarcophyton* samples (Table 5). In contrast, the bleached samples showed a drastic decline in photosynthetic performance. Elevated temperatures are one of the major contributing factors of coral bleaching events which may prompt photosynthetic dysfunction and loss of zooxanthellae cells (Michalek-Wagner and Willis 2001; Chavanich et al. 2009). High temperatures (30°C) were recorded across the sampling site during the study. This might suggest that the use of light energy for metabolic processes was impaired mostly likely due heat induced loss or disturbance of symbiotic zooxanthellae. Concurring with past studies which have also reported on the negative impact of elevated temperature on the photophysiology of the genera *Sarcophyton* (Chavanich et al. 2009; Baum et al. 2016).

Perhaps of most interest, samples from both conditions, healthy and bleached, showcased Similar Non-Photochemical Quenching (NPQ) activity. The non-photochemical quenching is a crucial protective mechanism adapted by phototrophs to dissipate excess light energy (radiation) through heat dissipation to protect the photosystem II from damage (Schreiber and Klughammer 2008; Bhagooli 2010; Bhagooli et al. 2021). Having similar quenching values imply that the symbionts or pigments may remain in the bleached soft coral sample hence the functioning of the protective mechanism. The high NPQ in the healthy samples suggests, however, that even these corals were experiencing light stress and reacting by deploying energy dissipating defense. Just like NPQ durability has been recorded in certain scleractinian corals under bleaching scenarios (Bhagooli 2010; Bhagooli et al. 2021), NPQ or similar photoprotective responses have been observed in *Sarcophyton* studies such as Farag et al. (2021). The sustaining of NPQ mechanisms in *Sarcophyton* may be linked to genus resilience in response to bleaching for soft corals.

In conclusion, this study showcases clear special variability in soft coral distribution and highlights differential photophysiology performance of *Sarcophyton* sp. across Rodrigues Island. The water quality along with other environmental factors seemed to act as important factors influencing soft coral assemblages in a region with limited baseline data. Additionally, the observed retention in *Sarcophyton* sp. protective mechanisms underscores its resistance to environmental stressors such as high temperatures. It also suggests their capacity to recover from bleaching stress, considering the possible presence of recovering symbiont. The findings highlight the ecological importance and adaptive strategies of soft corals in changing habitat conditions. The shifts in benthic reef communities from hard coral to soft coral emphasize the importance for adequate monitoring and further studies regarding the resilience and ecosystem functioning of soft corals. A limitation of this study is that the sampling effort was a single-timepoint and not longitudinal or repeated, which limits its generalization. The imprecision of the data set is still useful as a preliminary baseline for Rodrigues soft corals community, which indicates the need for longer and broader temporal and spatial monitoring.

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Decadal variation in the *Tridacna* population at two marine protected areas in Rodrigues Island, Republic of Mauritius

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Abstract. *Ramah S, Kaullysing D, Soondur M, Taleb-Hossenkhan N, Bhagooli R. 2025. Decadal variation in the* Tridacna *population at two marine protected areas in Rodrigues Island, Republic of Mauritius. Indo Pac J Ocean Life 9: 165-171.* Giant clams (Tridacninae) are largely threatened worldwide, but information regarding their distribution and abundance is limited in the Western Indian Ocean, especially in the waters of the Republic of Mauritius, including the island of Rodrigues. This study provides the first decadal assessment (2015-2024) of the population density of *Tridacna maxima* and *T. squamosa* within two marine protected areas: Southeast Marine Protected Area (SEMPA) and English Bay Marine Reserve (EBMR) found in Rodrigues Island. Annual surveys were carried out by placing five permanent belt transects of 50 m × 5 m (250 m²) at both sites. The data were extrapolated to individuals per hectare (ind./ha), and Mixed-effect models were used to assess temporal and spatial differences. Across the 10 years, SEMPA consistently supported higher *Tridacna* densities than EBMR, particularly for *T. maxima* (peak 640 ind./ha vs. 360 ind./ha). Species identity and interactions were significant, with *T. squamosa* occurring only in SEMPA, ranging from 13 to 120 ind./ha, and was absent from EBMR throughout the study. Statistical analyses revealed significant effects of site and species identity, as well as strong site × species and year × species interactions, indicating that temporal dynamics differed remarkedly between species and between MPAs. Surveys revealed significant site- and species-specific variations in giant clam densities in Rodrigues. Mean densities of *T. maxima* and *T. squamosa* were significantly higher in SEMPA compared to EBMR ($p<0.001$). Both species persisted across survey years in SEMPA, whereas densities in EBMR remained consistently low with no significant increase over time ($p=0.01$). These results indicate spatial heterogeneity in population trajectories and identify SEMPA as a key area of persistence. The findings of this study provide baseline evidence of site- and species-specific variation in giant clam populations in Rodrigues, contributing to broader understanding of spatial heterogeneity and long-term dynamics for future comparative research in the Western Indian Ocean.

Keywords: Giant clams, density, *Tridacna maxima*, *T. squamosa*, Rodrigues

Abbreviations: MPAs: Marine Protected Areas, WIO: Western Indian Ocean

INTRODUCTION

Giant clams (subfamily Tridacninae) were once abundant across Indo-Pacific reef ecosystems, where they contributed significantly to reef structure, productivity, and biodiversity (Neo et al. 2015; Ramah et al. 2019). However, decades of uncontrolled harvesting, habitat degradation, and accelerating climate change have driven widespread population declines, with some species now locally extinct in parts of their former range (Neo et al. 2017; Ramah et al. 2019; Fauvelot et al. 2020). Larger species such as *Tridacna gigas* have become functionally extinct in several regions due to unsustainable exploitation (Neo et al. 2017). In recognition of these threats, the International Union for Conservation of Nature (IUCN) lists multiple giant clam species as "Vulnerable," and all are included under Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES), regulating international trade (UNEP 2014). Despite these international designations, population trajectories continue to decline in many regions, indicating that legal protection alone is insufficient without effective local enforcement, habitat protection, and long-term ecological monitoring.

Despite their ecological importance, data on giant clam distribution and abundance remain limited in the Western Indian Ocean (WIO). While Pacific nations have implemented conservation measures such as minimum catch sizes, export monitoring, and aquaculture programs (Van Wynsberge et al. 2013; Purcell et al. 2020), comparable initiatives in the WIO are scarce. Mauritius represents one of the few countries in the region where giant clam populations have been studied, with surveys between 1999 and 2016 documenting significant declines in *Tridacna maxima* and *T. squamosa* densities, irrespective of protection status (Ramah et al. 2019). These findings highlight the urgent need for baseline data to inform management strategies, particularly in Rodrigues, where traditional fishing practices and climate stressors intersect. Rodrigues Island remains especially underrepresented in long-term ecological datasets, despite its strategic position within the Mascarene archipelago and its extensive shallow reef-flat habitats that are potentially suitable for giant clam persistence and recovery.

Ecologically, Tridacnines play a foundational role in reef ecosystems. Their symbiosis with photosynthetic zooxanthellae enhances primary productivity and nutrient cycling, while dense aggregations increase reef heterogeneity, provide substrate for epibionts, and shelter commensal organisms (Neo et al. 2015; Fauvelot et al. 2020). Their tissues and excretions also serve as food sources for predators and scavengers, reinforcing their importance in reef trophic dynamics (Ramah et al. 2019). By actively filtering seawater and recycling nutrients, giant clams influence local biogeochemical processes and contribute to the stability and functioning of coral reef ecosystems, particularly in shallow lagoon environments. Although giant clams are also culturally and commercially significant, valued for their meat, shells, and ornamental uses in Asia, the Pacific, and Mauritius (Wabnitz et al. 2003; Larson 2016; Purcell et al. 2020; Ramah et al. 2019), these practices have contributed to localized overexploitation. In Mauritius, where giant clams are known as “Bénitiers,” they hold cultural and artisanal importance but remain vulnerable to illegal harvesting despite legal protection under the Fisheries Act 2023 (Ramah et al. 2023). This tension between cultural use and conservation underscores the need for site-specific management approaches that balance livelihoods with ecological sustainability.

To address these gaps, this study focuses on giant clam populations in Rodrigues. We hypothesized that the South East Marine Protected Area (SEMPA) would support higher and more stable densities of *T. maxima* and *T. squamosa* compared to the English Bay Marine Reserve (EBMR), due to stronger enforcement, larger reef-flat area, and superior habitat conditions. Furthermore, we expected *T. squamosa* to exhibit greater temporal variability than *T. maxima*, reflecting its more specific substrate requirements and lower overall abundance (Neo et al. 2017; Fauvelot et al. 2020). By adopting a decadal monitoring framework based on permanent transects, this study seeks to capture both spatial contrasts and long-term temporal dynamics that are often missed in short-term surveys. By testing these hypotheses, this study aims to provide critical baseline data for the WIO and contribute to improved conservation strategies for giant clams in Rodrigues. Such baseline information is essential for evaluating the effectiveness of marine protected areas, guiding restoration or restocking initiatives, and supporting adaptive management under increasing environmental and anthropogenic pressures.

MATERIALS AND METHODS

Study sites

Rodrigues is a small volcanic island situated within the Western Indian Ocean, approximately 600 km east of Mauritius at 19.7245° S, 63.4272° E (Middleton and Burney 2013) (Figure 1). Similar to Mauritius and the Reunion Islands, Rodrigues forms part of the Mascarene Islands. It is approximately 18 km long and 6.5 km wide, and a fringing coral reef encloses a large, shallow lagoon (typically less than 1 m deep at low spring tide). The lagoon is characterized by extensive reef flats composed of calcareous substrates and sandy patches, creating heterogeneous habitats for benthic organisms. Coral cover is highest along reef crests and patch reefs, while inner lagoon areas are often subject to sedimentation and reduced coral growth (Bhagooli and Kaullysing 2019). Hydrodynamic conditions are strongly influenced by tidal exchange through narrow reef passes, resulting in limited water circulation and pronounced gradients in turbidity and nutrient availability.

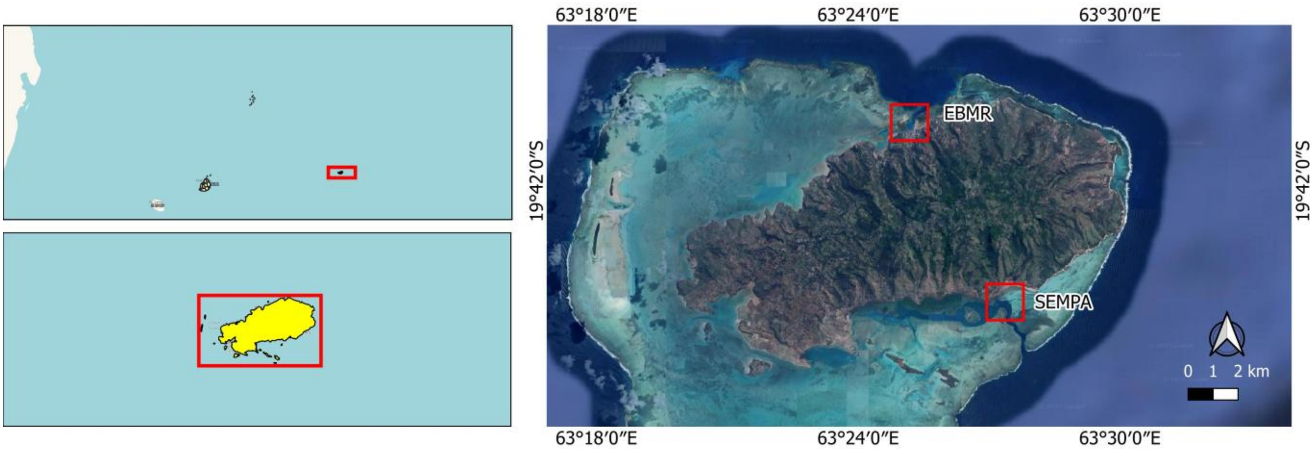

Figure 1. Map of Rodrigues Island, Republic of Mauritius (19.7245° S, 63.4272° E) showing the two surveyed sites – South East Marine Protected Area (SEMPA) and English Bay Marine Reserve (EBMR)

The two Marine Protected Areas (MPAs) in Rodrigues (Figure 1) differ in both environmental characteristics and management regimes. The South East Marine Protected Area (SEMPA), established under the Fisheries and Marine Resources – SEMPA Regulations 2011, encompasses a large reef-flat area with higher coral cover and diverse benthic substrates. SEMPA is demarcated into zones for different activities under strict control, and enforcement is comparatively stronger. The English Bay Marine Reserve (EBMR), scheduled under the Rodrigues Regional Assembly (Fisheries and Marine Resources – Marine Reserves) Regulations 2007, is smaller in spatial extent, with narrower reef flats and lower coral cover. Hydrodynamic conditions in EBMR are more constrained, and enforcement has historically been weaker. These differences in reef-flat size, habitat quality, and enforcement regimes provide the ecological and management context for testing hypotheses on species-specific population dynamics of *T. maxima* and *T. squamosa*.

Temporal population assessment

Underwater surveys were carried out by snorkeling yearly during April to June over a span of 10 years, from 2015 to 2024, at the two reef flat sites using a methodology adapted from Tisera et al. (2012). Five permanent belt transects of 50 m × 5 m (250 m^2) were laid at depths between 1 and 3 m, with 10 m spacing between each transect. Surveys were conducted during daylight hours and timed to coincide with mid- to low-tide states, when reef flats were most accessible and water depth allowed clear visual inspection. Substrate composition along transects included calcareous reef pavement, sandy patches, and scattered coral colonies. Visibility conditions varied between sites, influenced by lagoon hydrodynamics and sediment resuspension. Average underwater visibility ranged from 5 to 12 m, but occasional turbidity events reduced detectability of smaller giant clams, particularly in EBMR.

Surveys were restricted to calm sea states to minimize observer bias due to surface agitation. Detectability was further influenced by clam size and cryptic positioning within crevices or beneath coral overhangs, which may have led to underestimation of juvenile or partially buried individuals. To reduce observer bias, the same survey team conducted all transects across years, and permanent markers ensured consistent spatial coverage. Transects were fixed in location and re-surveyed annually to ensure comparability across years, resulting in a consistent sampling effort of 5 transects × 2 sites × 10 years = 100 transect-year combinations. Two species of giant clams were identified in situ based on their shell structure, morphology, and substrate affinity (Ramah et al. 2017), namely *T. maxima* and *T. squamosa*. To minimize inter-observer variability, surveys were conducted by trained observers following standardized protocols, with calibration exercises at the start of each field season. Potential species misidentification was mitigated by cross-checking uncertain records against photographic evidence and reference guides, and uncertain cases were recorded at the next reliable taxonomic level. Surveys were carried out every year during the same period. The results were expressed in individuals per hectare (ind./ha) for ease of comparison with other studies. The approximate reef-flat areas of each site were 979,296 m^2 and 90,355 m^2 for SEMPA and EBMR, respectively.

Statistical analyses

Model assumptions (normality of residuals, homoscedasticity, independence) were tested using diagnostic plots and formal tests. Residual normality was evaluated using the Shapiro–Wilk test and Q–Q plots, which indicated no significant deviations from normality (Shapiro–Wilk $W=0.98$, $p=0.21$). Homogeneity of variances was assessed using Levene's test, which showed no evidence of heteroscedasticity ($F=1.12$, $p=0.29$). Independence was confirmed through inspection of residual plots, which did not reveal temporal or spatial autocorrelation. These diagnostics support the validity of the mixed-effects models. However, environmental covariates (e.g., habitat, climate) were not included in the models, which constrains the strength of the mechanistic interpretation of the observed temporal and spatial patterns. Statistical analysis was performed using R (version 4.x; R Core Team). Mixed-effects models were fitted using the lme4 package, with year, sites, and species identity specified as fixed effects and sites included as a random intercept to account for repeated annual measures. Model significance was assessed using Type III Wald χ^2 tests via the car package, and effect sizes (r^2) were calculated to quantify the magnitude of observed effects. Results are presented as mean individuals per hectare (ind./ha).

RESULTS AND DISCUSSION

Results

SEMPA consistently supported the highest recorded densities of both *T. maxima* and *T. squamosa* across surveyed sites in Rodrigues over the past decade. In 2021, SEMPA exhibited peak densities of 640 ind./ha for *T. maxima* and 120 ind./ha for *T. squamosa*. In contrast, the lowest density of *T. maxima* was recorded at EBMR in 2017, with only 120 ind./ha, highlighting spatial variability in population abundance and possible differences in habitat quality or enforcement effectiveness. Over the ten-year monitoring period, the lowest densities of *T. squamosa* were also observed at SEMPA in 2018, with a count of 13 ind./ha (Figure 2). Notably, no individuals of *T. squamosa* were recorded along any surveyed transects in EBMR throughout the entire decade (Figure 3), underscoring a potential local extinction or severe population bottleneck in that reserve.

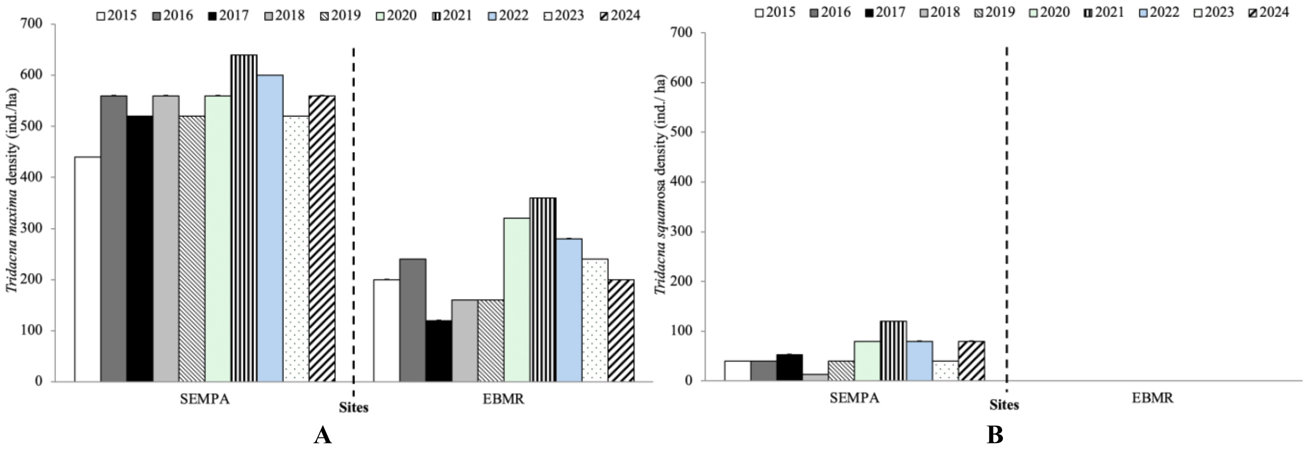

Figure 2. Temporal variation in population density (individuals per hectare) of A. *Tridacna maxima* and B. *T. squamosa* at South East Marine Protected Area (SEMPA) and English Bay Marine Reserve (EBMR). Bars represent Mean (n=10 years of data collected)

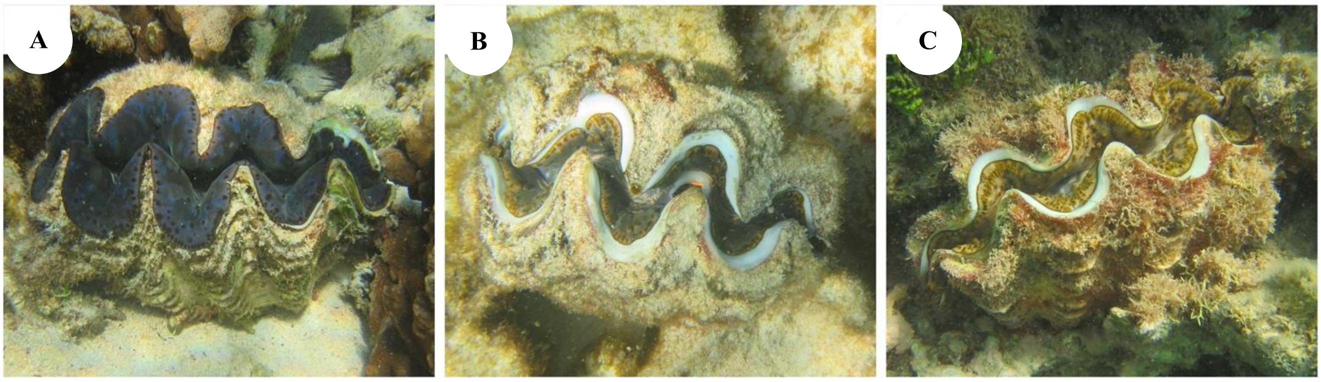

Figure 3. *Tridacna maxima* and *T. squamosa* were observed at the South East Marine Protected Area (SEMPA) and the English Bay Marine Reserve (EBMR). A and B. *Tridacna maxima* observed at SEMPA and EBMR, respectively, C. *Tridacna squamosa* observed at SEMPA only

The analysis revealed a highly significant main effect of site, with SEMPA consistently supporting higher densities of *Tridacna* than EBMR across all years ($p<0.001$, $r^2=0.70$). This difference was evident in both species, but particularly pronounced for *T. maxima*, which reached peak densities of 640 ind./ha in SEMPA during 2021, compared to a maximum of 360 ind./ha in EBMR. A significant main effect of species identity was also observed ($p=0.01$, $r^2=0.30$). *T. maxima* was dominant in SEMPA, while *T. squamosa* occurred at lower densities and was completely absent in EBMR. Within SEMPA, *T. squamosa* fluctuated considerably across years, ranging from 13 ind./ha in 2018 to 120 ind./ha in 2021.

The main effect of year was marginal ($p=0.07$, $r^2=0.28$), reflecting moderate fluctuations in species densities across the studied period. These fluctuations were most evident in SEMPA, where both species showed temporal variability, while EBMR remained relatively stable with consistently low counts. Interaction effects provided further insight into site specific and species-specific dynamics. The site × species interaction was strong ($p<0.01$, $r^2=0.45$), confirming that EBMR supported only *T. maxima* while SEMPA supported both species. The year × species interaction was significant ($p=0.05$, $r^2=0.32$), indicating that *T. squamosa* exhibited greater temporal variability than *T. maxima*. Finally, the year × site × species interaction was significant ($p=0.04$, $r^2=0.36$), demonstrating that species responded differently to temporal variation depending on site (Table 1). Although overall densities remain low compared to regional benchmarks, the values recorded here fall within the range reported from other Indian Ocean sites. For example, *T. maxima* densities in the Indian Ocean and Southeast Asia range from 10 to 300 individuals per hectare (Apte et al. 2010; Chi et al. 2025), yet Mauritius consistently reports values at the lower end of this spectrum.

Table 1. Mixed-effects models of *T. maxima* and *T. squamosa* densities at different sites within ten years (2015 to 2024)

Effect	**df**	**X²**	**p-value**	**r²**
Sites	1, 18	50	<0.001	0.70
Species	1, 18	08	0.01	0.30
Year	10, 18	2.5	0.07	0.28
Site × Species	1, 18	15	<0.01	0.45
Year × Species	10, 18	2.8	0.05	0.32
Year × Site × Species	10, 18	3.1	0.04	0.36

Discussion

The study revealed consistent and significant contrasts between SEMPA and EBMR, underscoring the importance of site-level ecological conditions and governance in shaping giant clam populations. SEMPA supported peak densities of *T. maxima* (640 ind./ha in 2021) and *T. squamosa* (120 ind./ha in 2021), while EBMR recorded much lower values, with *T. maxima* reaching only 360 ind./ha at its maximum and *T. squamosa* absent throughout the decade. These findings suggest that SEMPA's ecological integrity and enforcement capacity provide a more favorable environment for clam persistence, whereas EBMR's consistently low densities point to structural limitations in habitat quality, recruitment success, or enforcement effectiveness. While SEMPA may be approaching a plateau in carrying capacity, EBMR appears to remain in a recruitment-limited or colonization phase. This divergence highlights the need for tailored management: SEMPA's role as a refuge should be consolidated, while EBMR requires targeted interventions to overcome bottlenecks.

Regional comparisons further contextualize these results. In Thailand, *T. maxima* densities have been reported at 400-700 ind./ha (Mehrotra et al. 2021), while Malaysia records values of 250-500 ind./ha (Lee et al. 2024). Against these benchmarks, SEMPA's peak of 640 ind./ha is comparable to healthier ecosystems, whereas EBMR's maximum of 360 ind./ha remains below regional averages. This contrast reinforces the conclusion that site-specific governance and ecological conditions directly influence population trajectories. The two focal species exhibited distinct ecological responses. *T. maxima* was present at both sites, albeit at densities lower than regional benchmarks, suggesting resilience but also vulnerability to recruitment limitations and anthropogenic pressures (Apte et al. 2010; Chi et al. 2025). Its broader distribution indicates adaptability to variable habitats, though reduced densities highlight ecological stress. In contrast, *T. squamosa* was restricted to SEMPA, fluctuating between 13 ind./ha in 2018 and 120 ind./ha in 2021. Its absence from EBMR suggests either local extinction or severe recruitment failure. The species' close association with coral habitats (Ramah et al. 2017) underscores its dependence on reef structure for anchorage and survival, making it particularly vulnerable to coral degradation and explaining its restricted distribution and greater temporal variability. These species-specific differences highlight the need for differentiated conservation strategies: *T. maxima* populations may benefit most from enforcement and recruitment support, while *T. squamosa* requires habitat restoration and coral protection to ensure persistence.

Temporal variability was evident across survey years, particularly for *T. squamosa* in SEMPA. Fluctuations ranged from very low densities (13 ind./ha in 2018) to higher values (120 ind./ha in 2021), reflecting sensitivity to environmental variability and recruitment dynamics. *T. maxima*, by contrast, showed more stable trends, with moderate increases over time. Recruitment success appears density-dependent, consistent with the Allee effect, whereby low adult densities hinder fertilization and larval settlement (Neo et al. 2015; Bay et al. 2023). This mechanism explains the persistence of low densities in EBMR and the variability observed in SEMPA. Juveniles remain particularly vulnerable to predation and environmental stress (Soo and Todd 2014; Ramah et al. 2019), further constraining recovery. A slight increase in densities in 2021 across both sites may reflect reduced anthropogenic pressure, but attributing this directly to COVID-19 restrictions is speculative. While global reports suggest wildlife resurgence during lockdowns (Bar 2020), local evidence remains insufficient. The observed uptick should therefore be interpreted cautiously, as part of broader temporal variability rather than a confirmed causal effect.

This study is subject to several limitations that constrain interpretation of the results. The potential under-detection of small or cryptic individuals may have led to underestimates of true population densities, a challenge noted in giant clam surveys where juveniles are easily overlooked due to their cryptic behaviour and small size (Neo et al. 2013). The absence of environmental covariates such as water quality, temperature, or reef condition restricts the ability to link observed population trends to ecological drivers, despite evidence that hydrodynamics, habitat quality, and climate variability strongly influence recruitment and dispersal success (Van Wynsberge et al. 2017). Variance estimates also remain uncertain, and the lack of demographic or size-structure data limits insights into recruitment dynamics and population age profiles, which are critical for assessing long-term resilience (Soo and Todd 2014). However, the results of this study have enough evidence to highlight the importance of enforcement and surveillance in sustaining giant clam populations. SEMPA's consistently higher densities of both *T. maxima* and *T. squamosa* demonstrate the effectiveness of strong institutional support and active monitoring (Ramah et al. 2019). By contrast, EBMR's weaker performance underscores the need to strengthen enforcement capacity. Similar findings have been reported in Indo-Pacific MPAs, where effective enforcement correlates with higher clam densities and reduced exploitation (Van Wynsberge et al. 2016). Enhancing surveillance and compliance mechanisms in EBMR could therefore reduce harvesting pressure and improve recruitment outcomes, aligning conservation efforts with national blue economy objectives.

Restocking and seeding programs also emerge as critical interventions for EBMR, where *T. squamosa* was absent throughout the decade and *T. maxima* densities remained comparatively low. Restocking has been successfully applied in other regions, such as Micronesia and Palau, where hatchery-reared clams were used to replenish depleted populations (Neo et al. 2015; Larson 2016). Targeted restocking, combined with habitat enhancement, could help overcome recruitment bottlenecks and re-establish viable populations. Such measures would be particularly important in areas where natural recovery appears constrained by low adult densities and the Allee effect, which limits reproductive success at reduced population sizes (Bay et al. 2023). Habitat restoration is equally essential, particularly for *T. squamosa*, whose survival is closely linked to coral reef structure. The species' dependence on branching and tabular corals for anchorage and protection means that reef degradation directly undermines its persistence (Ramah et al. 2017). Restoration initiatives that enhance coral cover and structural complexity would therefore provide the microhabitats necessary for settlement, juvenile survival, and adult reproduction. Evidence from Southeast Asia shows that reef restoration projects can improve settlement success and increase clam survival rates (Mehrotra et al. 2021; Lee et al. 2024). These efforts would not only benefit giant clams but also contribute to broader reef ecosystem resilience.

Finally, long-term monitoring remains indispensable for adaptive management. The temporal variability observed in SEMPA, especially for *T. squamosa*, highlights the need for sustained ecological surveys to capture fluctuations and assess the effectiveness of interventions. Complementary genetic studies could provide insights into population connectivity, resilience, and adaptive potential, informing strategies for restocking and habitat restoration (Neo and Todd 2013; Van Wynsberge et al. 2017). By integrating ecological monitoring with targeted interventions, management can better respond to site-specific challenges and ensure the long-term persistence of giant clam populations.

In conclusion, this decadal assessment revealed clear site- and species-specific differences in giant clam populations around Rodrigues Island. Statistical analyses demonstrated significant effects of site and species identity, with interaction terms indicating that temporal dynamics varied between marine protected areas and between *Tridacna* species. SEMPA consistently supported higher and more stable densities, underscoring its role as a key refuge, whereas EBMR exhibited persistently low densities and limited recovery potential under current conditions. These contrasting trajectories highlight the importance of site-specific ecological conditions and governance, suggesting that effective enforcement and habitat integrity are critical for sustaining giant clam populations. Interpretation of these patterns is constrained by methodological limitations, including potential underdetection of cryptic individuals, the absence of environmental covariates, and the lack of demographic or size-structure data. Future studies should integrate habitat and climate variables, monitor size classes, and incorporate genetic analyses to better understand recruitment, connectivity, and resilience. Targeted rehabilitation or reseeding, particularly in EBMR, alongside strengthened enforcement and sustained monitoring, may support long-term population recovery in Rodrigues.

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