

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 remarkably 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.

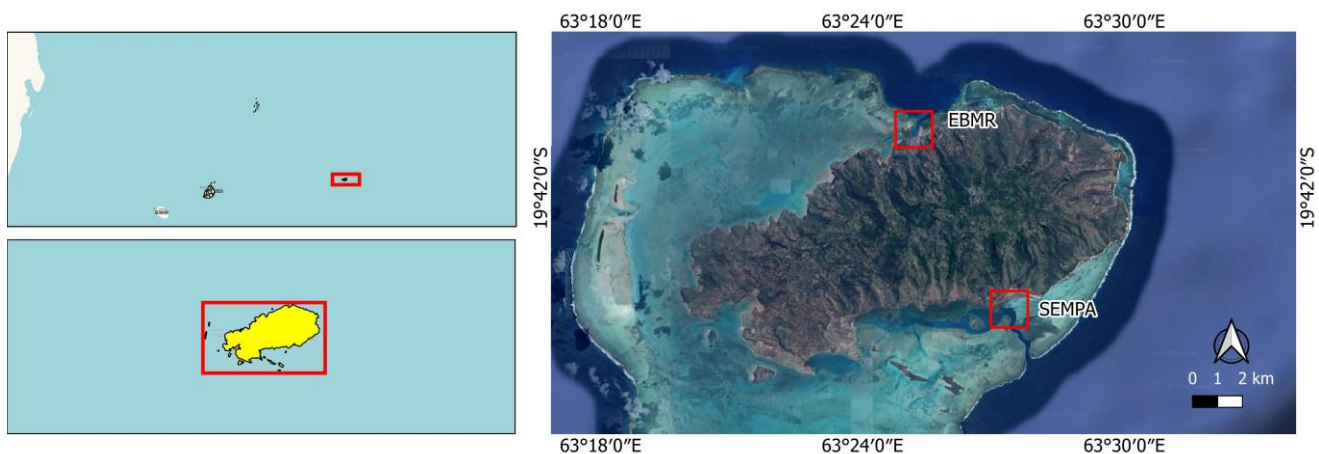


Figure 1. Map of Rodrigues Island, Republic of Mauritius (19.7245° S, 63.4272° E) showing the two surveyed sites – South East Marine Protected Area (SEMPA) and English Bay Marine Reserve (EBMR)

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 m²) 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 m² and 90,355 m² 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.

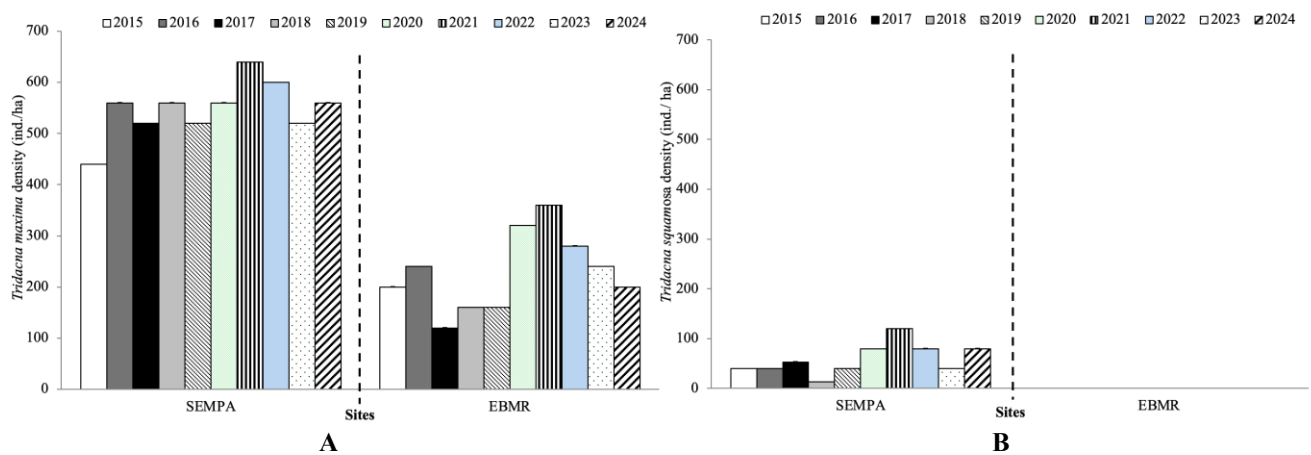


Figure 2. Temporal variation in population density (individuals per hectare) of A. *Tridacna maxima* and B. *T. squamosa* at South East Marine Protected Area (SEMPA) and English Bay Marine Reserve (EBMR). Bars represent Mean (n=10 years of data collected)

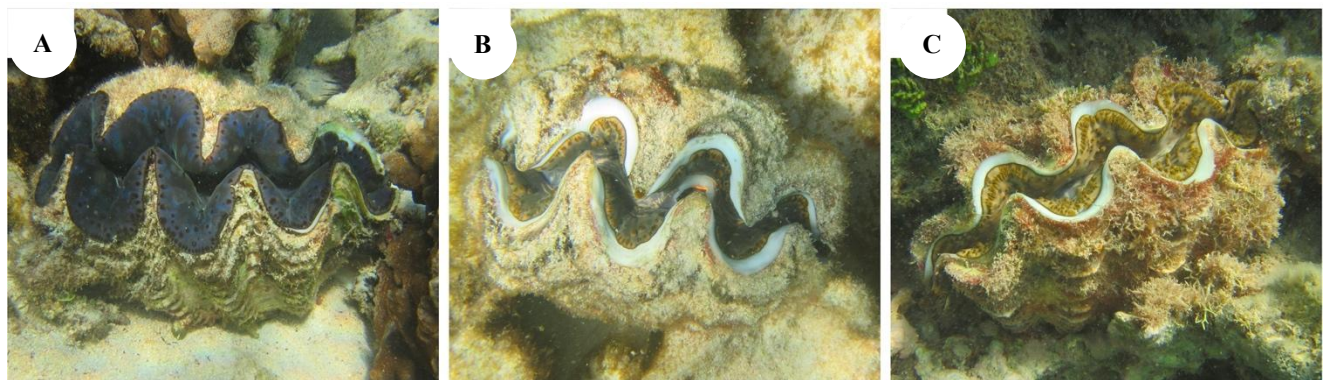


Figure 3. *Tridacna maxima* and *T. squamosa* were observed at the South East Marine Protected Area (SEMPA) and the English Bay Marine Reserve (EBMR). A and B. *Tridacna maxima* observed at SEMPA and EBMR, respectively, C. *Tridacna squamosa* observed at SEMPA only

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 \times 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 \times 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 \times site \times 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 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	X ²	p-value	r ²
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 \times Species	1, 18	15	<0.01	0.45
Year \times Species	10, 18	2.8	0.05	0.32
Year \times Site \times 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 reseeded, particularly in EBMR, alongside strengthened enforcement and sustained monitoring, may support long-term population recovery in Rodrigues.

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