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RESEARCH ARTICLE

Restoring *Halodule uninervis*: evaluating planting methods and biodiversity

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Seagrass provides a crucial habitat for numerous marine species and serves as a vital food source for endangered species, like dugongs. While extensive research on restoration has been conducted on certain temperate and slow-growing climax seagrass species, limited attention has been given to tropical pioneer species. This study aimed to assess and compare two restoration methods for the pioneer seagrass *Halodule uninervis* and evaluate their potential for biodiversity recovery after planting. We conducted a field experiment at subtropical Inhaca Island, southern Mozambique, testing the efficiency of two planting methods (plugs and single shoots) and two planting densities (∼100 and ∼300 shoots/m^2). We monitored seagrass shoot density in two sites for 16 months, and benthic macrofauna density for 12 months. Results demonstrated that seagrass could grow in all combinations of planting methods and densities in both sites. Specifically, the single shoot method at the high-density treatment proved the most effective, resulting in approximately 1000 shoots/m^2 within a year. Faunal densities, primarily dominated by polychaetes followed by malacostraca, bivalves, and gastropods, indicated rapid colonization of the planted areas, especially in the high-density treatments. Our findings suggest that restoring *H. uninervis* is feasible using the two tested planting methods. This is particularly significant because *H. uninervis* is a preferred dugong food source, and its decline due to anthropogenic activities could be reversed through restoration efforts. Nonetheless, conserving existing seagrass should be the primary focus, and restoration approaches should be employed as a valuable tool for managing coastal areas.

Key words: coastal habitat management, *Halodule uninervis* restoration, infauna colonization, seagrass biodiversity recovery, seagrass restoration techniques

Implications for Practice

- Restoration techniques as plug and single shoot planting are feasible restoration methods for the pioneer seagrass species *Halodule uninervis*, with high-density yields, suggesting its adoption in future restoration projects.
- Successful restoration can result in rapid colonization of planted areas by fauna, highlighting the potential of restored seagrass habitats to support marine biodiversity.
- *Halodule uninervis* is a preferred food source of *Dugong dugon*, classified by World Conservation Union as vulnerable species; hence restoration efforts could significantly benefit dugong populations by restoring their feeding grounds.

Introduction

Seagrass ecosystems rank among the most productive and diverse marine ecosystems globally, providing essential ecosystem functions and supporting a wide range of marine species (Duffy 2006; Barbier et al. 2011). Despite their ecological significance, seagrass faces a global decline due to both natural events (e.g. storms, hurricanes, and diseases) and human-induced activities (e.g. dredging and filling, pollution, coastal development, boating, and fishing practices) (Hughes et al. 2009; Waycott et al. 2009).

In Mozambique as a whole, seagrass decline has been observed in various coastal areas and is primarily due to cyclone activity, floods, and shellfish fisheries (Bandeira et al. 2021; Amone-Mabuto et al. 2023), where the Western Maputo Bay has experienced a reduction of seagrass by 7% a year

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between 1992 and 2003 (Bandeira et al. 2021). The island of Inhaca in southern Mozambique is home to a diverse range of seagrass species, including *Halodule uninervis*, a key food source for dugongs in the Western Indian Ocean region (Findlay et al. 2011; Fernando et al. 2014). *Halodule uninervis* is of key importance as an ecosystem-building pioneer species, growing in intertidal and subtidal zones in both sheltered and exposed areas, either as a single species or mixed with other seagrass species (Bandeira et al. 2014).

In addition, seagrass meadows at Inhaca Island also provide habitat for a wide range of other marine species, supporting local fisheries, including fish, crustaceans, and mollusks (Nordlund & Gullström 2013). The small-scale fisheries surrounding Inhaca Island are vital for local communities, providing both food and income. Many of these fisheries rely on seagrass meadows for productivity (Nordlund & Gullström 2013; Chitará-Nhandimo et al. 2022).

Due to the high value and accelerating loss of seagrass meadows worldwide, there is an increasing need for effective restoration approaches for seagrass ecosystems (Cunha et al. 2012). Restoring seagrass meadows can contribute to maintaining (or recovering) biodiversity, supporting fisheries, and mitigating the impacts of climate change (e.g. through coastal protection). However, developing targeted restoration techniques for specific seagrass species is essential for sustaining successful long-term restoration programs (Van Katwijk et al. 2016; Tan et al. 2023; Nordlund et al. 2024). While a great effort has been directed toward developing restoration methods for seagrass species such as the temperate seagrass *Zostera marina* (Orth et al. 2010, 2012; Eriander et al. 2016; Gagnon et al. 2023) and the Mediterranean climax seagrass species *Posidonia oceanica* (Domínguez et al. 2012; Alagna et al. 2019; Escandell-Westcott et al. 2023), there is a need for attention to restoration methods also for tropical seagrass and pioneer species, particularly in the understudied Western Indian Ocean region, despite some seagrass restoration trials in Kenya (e.g. Uku et al. 2022), Tanzania (e.g. Wegoro et al. 2022) and Mozambique (e.g. Amone-Mabuto et al. 2022).

The major aims of this study were to evaluate the effectiveness of restoration methods for seagrass *H. uninervis* to recover key ecosystem functions and assess potential changes in biodiversity after restoration. Specifically, we aimed to: (1) assess the efficiency of two different planting methods (plugs and single shoots) tested on two planting densities (100 and 300 shoots/m^2) for the growth of *H. uninervis*, and (2) assess macrofaunal colonization 1 year after the planting started. This information will contribute to supporting large-scale restoration projects as well as seagrass conservation and management interventions in the region.

Methods

A seagrass planting experiment was carried out in two sites at Inhaca Island, which is a small island situated in the outer edge zone of Maputo Bay and part of Maputo National Park, in southern Mozambique (Fig. 1). The shallow environment at Inhaca is supported by the large meadows present in the area (approximately 3943 ha) (Chitará-Nhandimo et al. 2022). At Inhaca,

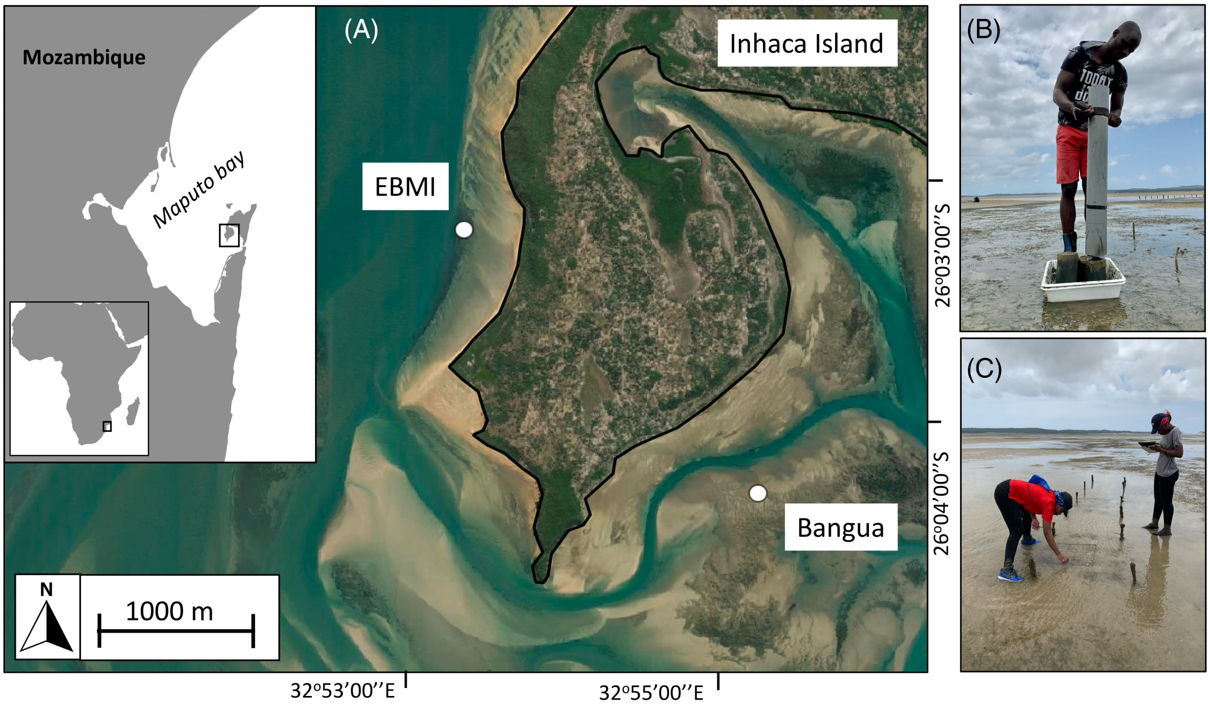

Figure 1. The island of Inhaca in Maputo Bay, Mozambique. (A) Planting locations in intertidal flats at Bangua and EBMI, (B) sediment plugs that were used for seagrass transplanting and fauna sampling, and (C) seagrass shoot counting at low tide with a quadrat to monitor growth rate after planting.

nine seagrass species are present, with *Halodule uninervis* being distributed in the higher intertidal area exposed to air for extended periods every day. The tides are semidiurnal and the tidal amplitude ranges between 0.1 and 3.9 m (de Boer & Longamane 1996). The water temperature varies within the extremes of 20–39°C, and salinity fluctuates within the range of 30–39 PSU (mean: 35 PSU) (Bandeira 2002).

Two sites were selected to conduct the seagrass transplantation, that is, Bangua, which is an area located at the southern bay of Inhaca, and an area near the Inhaca Marine Biological Station (EBMI) in the western part of the island (Fig. 1A). Bangua is characterized by intertidal flats and by narrow and shallow channels, connecting Maputo Bay and the Indian Ocean (de Boer et al. 2000; Canhanga & Dias 2005). The EBMI site is dominated by the seagrass *Thalassodendron ciliatum*. The western part of Inhaca is protected from strong currents and waves (Macnae & Kalk 1962; Kalk 1995). The southern bay of Inhaca is frequented by dugongs, utilizing the seagrass beds as feeding grounds (Cossa et al. 2023).

Experimental Design: Testing Restoration Methods

To assess transplant growth rate, two planting methods were tested: (1) *the plug method*, where a group of seagrass shoots was transplanted within intact sediment using cores (Fonseca et al. 1998), and (2) *the single shoot method*, where individual shoots were planted without sediment (Orth et al. 1999). Transplanting shoots with intact root-rhizome complexes anchored to the sediment using cores or sods is considered less stressful for the plants than using the single shoot strategy, leading to higher survival and growth rates (Fonseca et al. 1998). However, the plug transplantation method requires more effort for collecting, transporting, and deploying the sediment. In contrast, planting single shoots with bare roots and rhizomes is less labor-intensive and less expensive, but the plants may be more stressed during the manipulation process (Fonseca et al. 1998).

For the plug method, seagrass shoots were collected using an 11 cm inner diameter polivinyl choride (PVC) corer, extracting intact shoots and 15 cm of sediment (Fig. 1B) to increase the chance of survival and growth of transplanted seagrass (Van Keulen et al. 2003). Sediment plugs with shoots were planted within pre-made holes in the sediment surface of a similar size as the plugs. For the single shoot method, shoots were harvested by hand, with each shoot carefully picked by breaking off the rhizome 2–3 cm from the meristem of the apex shoot. Shoots were collected in bundles of 50 to facilitate the transport and counts. Shoots were planted as described by Orth et al. (1999) by pushing the single rhizome with two fingers into the sediment, enhancing the anchoring capacity of the sediment and minimizing the disturbance of the top sediment layer.

To explore the potential effect of canopy sheltering and self-sustaining density interactions on plant growth, tests were conducted using two planting densities, including a low-density treatment of 100 shoot/m^2 and a high-density treatment of 300 shoots/m^2. Each plug contained 10–25 shoots, with four plugs planted in the low-density treatment (approximately 100 shoots) and 16 plugs in the high-density treatment (~300 shoots). These planting densities represent 2 and 6% of the natural densities (~5000 shoots/m^2) recorded during the experiment.

Data Collection: Estimation of Shoot Density and Growth Rate. To evaluate the impact of seagrass harvesting using the plug method, the number of shoots was monitored at the donor locations and in the closest intact seagrass meadows. Seagrass shoot density was determined by counting the number of shoots inside 25 × 25 cm quadrats ($n = 3$) in intact seagrass meadows and in donor locations after 10 months of planting.

Shoots were collected in natural meadows near the planting site (within 100 m distance), transported in buckets, and planted ~2–2.5 hours after collection. At each planting site, three transects with square plots of 1 m^2 were set with three replicates per treatment. Plots were marked with wooden poles in the corners and labeled to facilitate monitoring (Fig. 2). Seagrass was planted in November 2019, and seagrass shoot density was monitored (Fig. 1C) once in May, July, September, and November of 2020, and March of 2021, identified as months 0, 6, 8, 10, 12, and 16, respectively.

Since *H. uninervis* is a fast-growing species, growth rate was used as a measure, indicating both the survival of initial shoots and the emergence of new shoots. The growth rate was then calculated as the percentage increase in the total number of shoots from the initial count, as follows:

$$\text{Growth rate} = \frac{\text{number of shoots at time } t - \text{number of initial shoots}}{\text{number of initial shoots}} \times 100 \qquad (1)$$

Benthic Macrofauna Colonization

Benthic macrofauna (infauna and epifauna) samples were collected using a PVC core (11 cm diameter and 15 cm length) in the plots. To minimize the impact of the core on subsequent samplings, the cores were taken in a clockwise pattern by dividing the plot in quadrats. One sediment sample was collected per plot ($n = 3$ per treatment) and directly transferred to plastic bags. Additionally, five cores were taken from the donor area and sandy area near the planting plots. In the laboratory, samples were sieved through a 0.5 mm mesh, and macrofauna was collected and preserved in 70% ethanol. Faunal specimens were identified to species or to the lowest taxonomic level possible and counted using a stereomicroscope. The sampling of fauna was performed in months 8, 10, and 12 in the high-density treatments on the same days as seagrass shoot density was monitored to capture both the establishment of fauna and the seasonal variations within the first year. We sampled in the high-density shoot treatments, assuming that faunal recovery is linear to recovery of the seagrass structure in terms of shoot density (Fonseca et al. 1996).

Sediment Composition and Water Temperature

Sediment composition was determined for both planting sites by sampling the top 5 cm layer ($n = 3$) and used as an indirect

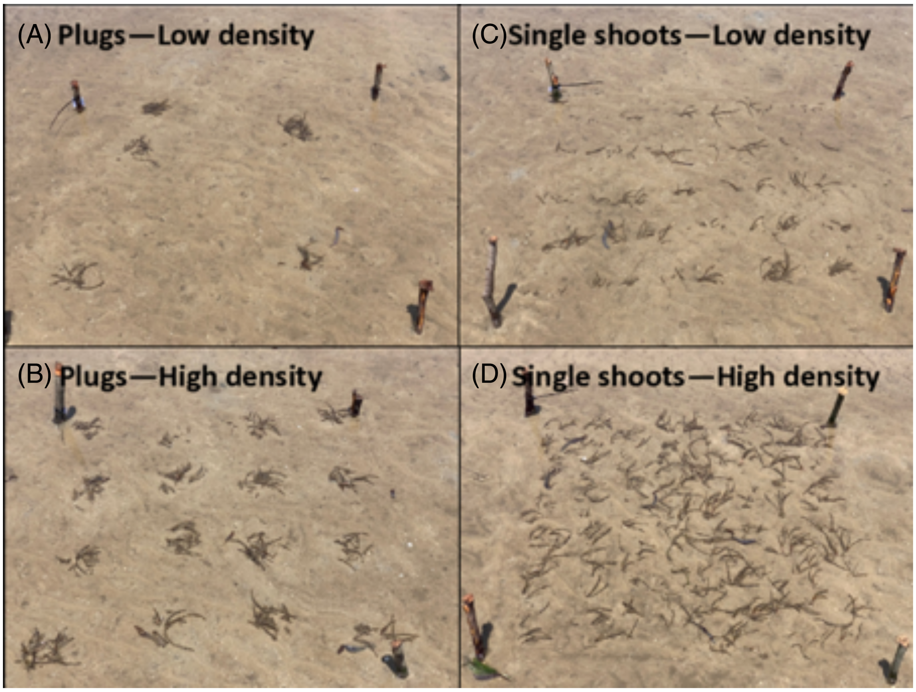

Figure 2. Initial planting configurations in the seagrass restoration experiment using sediment plugs (A, B) and single shoots (C, D), at low and high seagrass shoot densities.

indicator of wave and current exposure (Fonseca et al. 1983). The organic content of the sediment after large biomass removal (roots and rhizomes) was calculated by loss on ignition (LOI). This involved burning the samples at 450° C for 5 hours and measuring the difference in sample weight before and after burning. Grain size fractions were determined by sieving the sediment through a stack of sieves, and grain size diameter was calculated according to Blott and Pye (2001). The percentage of organic content was 0.82 ± 0.14 for Bangua and 1.31 ± 0.57 for EBMI. The sediment grain size analysis showed that both sites were composed of medium sand (D50: 309.5 μm for Bangua and 314.7 μm for EBMI).

Water temperature was recorded with data loggers (HOBO, UA-002-64, Onset®) at 15-minute intervals throughout the growth season. The loggers were regularly cleaned, and data were reviewed before analysis to remove unreliable measurements due to fouling and air exposure periods during low tide. The water temperature varied between 17.1 and 32.6°C in EBMI and between 17.0 and 32.8°C in Bangua during the planting period.

Statistical Analyses

Statistical analyses were conducted using R version 4.2.0. All data were checked for normality using a Shapiro–Wilk test ($\alpha = 0.05$), and homoscedasticity with Levene's test. To test for differences in shoot persistence and growth rate between the two methods (plug and single shoots) and the two densities (low and high) in both sites, a three-way analysis of variance (ANOVA) was performed. The average increase in seagrass shoot density from month 0 to month 16 served as the dependent variable, with plant method, plant density, and site as fixed independent variables. The difference between the donor and natural meadows in both sites was tested using a *t* test.

To assess fauna colonization capacity in restored sites, one-way non-parametric permutational multivariate analyses of variances (PERMANOVA) were used. Pairwise tests were subsequently performed to examine the differences in macrofaunal assemblage composition between the two high-density restoration plots after 8, 10, and 12 months, the natural *H. uninervis* meadow, and the bare sediment. The Bray–Curtis similarity measure was applied to fourth-root transformed data of macrofaunal abundances. Principal coordinates analysis (PCoA) was used to visually present the differences in macrofaunal assemblage composition.

Results

Shoot Density and Growth Rate

The transplanted *Halodule uninervis* showed an increase in shoot density in both tested methods (plug and single shoots) and the two densities (low and high) over the 16 months of the experiment at Bangua and EBMI (Fig. 3A). However, shoot densities were not consistently maintained over time in either of the two sites. At Bangua, experimental plots using both methods and in high densities showed an overall growth after 6 months (month 6) of transplantation, with an average percentage of shoot density increase of 102.9% using the plug method and 217.9% using the single shoot method. This trend continued

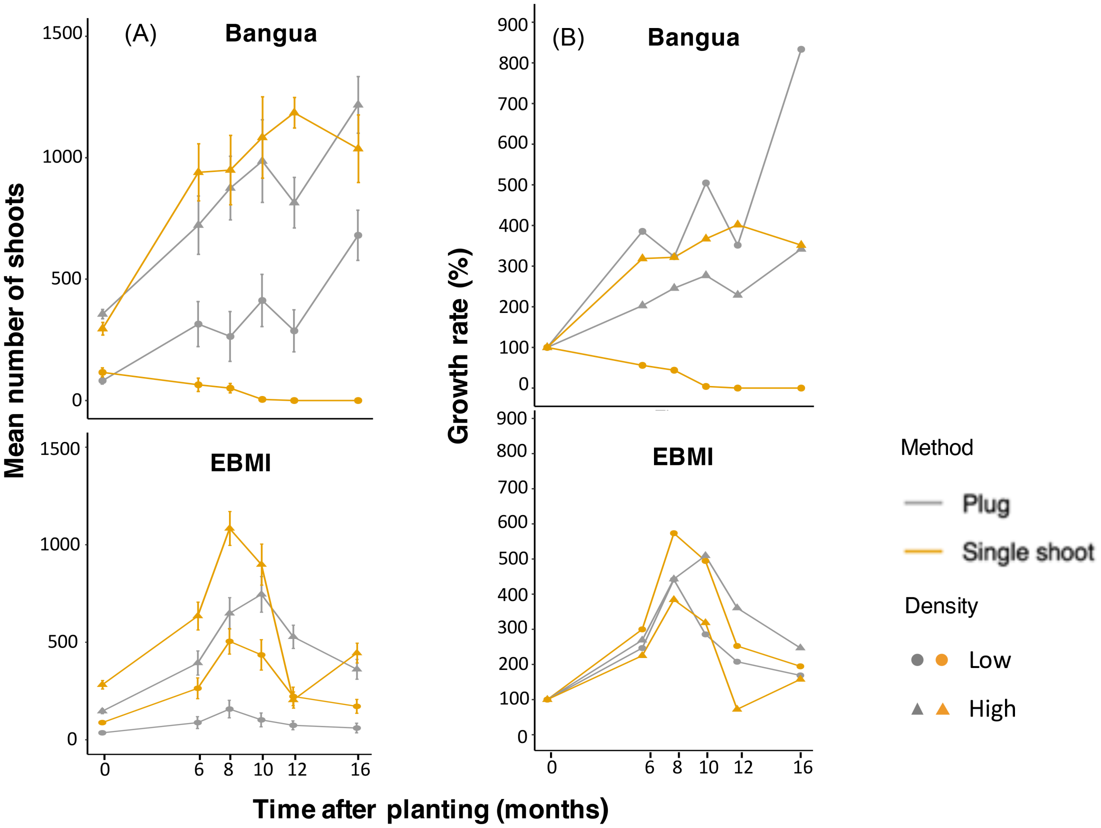

Figure 3. (A) Average number of seagrass shoots per m^2, and (B) Growth rate (%) of seagrass shoots after planting using both the plug and single shoot methods during the experimental period. Two initial planting densities were used (low: 100 shoot/m^2, and high: 300 shoot/m^2) at the two study sites, that is, Bangua and EBMI (Fig. 1). Values are mean ± SE ($n = 3$).

and remained relatively stable after 16 months, with an average percentage shoot density increase of 242.0% (plug) and 250.7% (single shoot), respectively. Plots transplanted using the plug method and low densities showed an increase in shoot density after 16 months, while plots with the single shoot method and low densities showed a decrease in shoot density over time, and all disappeared from the plots after 16 months.

At the EBMI site, a similar growth trend as in Bangua was observed in the treatments of both methods and densities, particularly in high-density plots, over the 16-month experiment. However, in months 10 and 12, a reduction in shoot density of 260.7 and 146.8%, respectively, was observed in the plug method. Further, a shoot density decrease of 27.8% was observed after 10 months, followed by an increase of 57.6% in the single shoot method when compared to the initially planted shoot density.

The average increase in seagrass shoot density in experimental plots after 16 months did not significantly differ between the two planting densities or between the two study sites. Additionally, there was no interaction effect between these three variables (Table S1).

The growth rate of seagrass shoots in the two study sites was not necessarily dependent on the method used or plant densities (Fig. 3B). At Bangua, the low-density plots using the plug method had a much higher growth rate after 16 months (833.4%) compared to the initial level (month 0), while the growth rate in the high-density plots using both the plug and single shoot methods were 342.0 and 351.5%, respectively. In EBMI, the growth rate at the end of the experiment was over 150% for both methods and the two tested planting densities.

The mean seagrass shoot density in the donor meadows at EBMI (1208.3 ± 355.3 shoots/m^2; mean ± SE) was not significantly different from the nearby natural meadows (504.7 ± 222.6) after 10 months of planting (t test, $p = 0.17$). In Bangua, the donor meadows were reaching a similar mean shoot density (3189.8 ± 421.9) to the nearby natural meadows (4967.6 ± 162.8). However, there were significant differences in shoot density between donor and natural meadows (t test, $p < 0.05$). This indicates a seagrass recovery from the impact of the plug method in both sites (Fig. 4).

Macrofauna Colonization

The macrofauna assemblage composition differed between the restored plots, the natural meadow and the bare sediment at both Bangua and EBMI (PERMANOVA: $F_{[3,35]} = 2.17, p < 0.0001$; $F_{[3,35]} = 1.85$, $p = 0.001$, respectively), and in both sites, the differences were mainly between the bare sediment and seagrass (restored and natural meadows). No significant differences were observed between restored and natural meadows at months

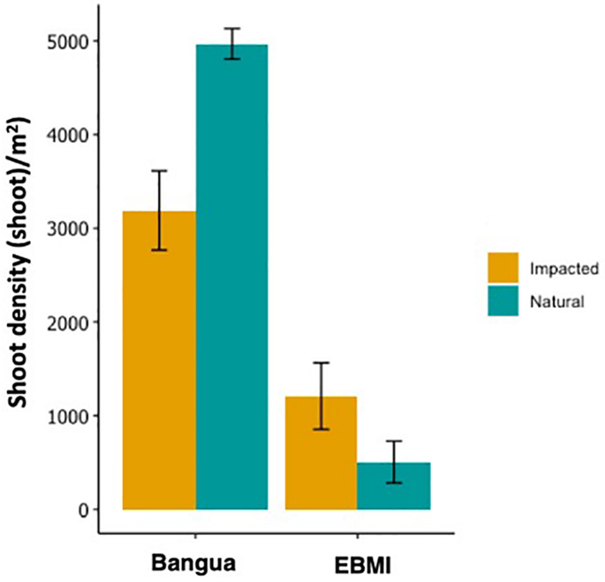

Figure 4. Seagrass shoot density in the impacted donor meadow compared to the natural meadow after 10 months of planting (month 10). Values are mean ± SE ($n = 3$) (Bangua: $p < 0.05$; EBMI: $p = 0.17$).

8, 10, and 12 in the EBMI site ($F_{[2,35]} = 1.16$, $p = 0.25$), while in Bangua differences were verified between months 8 and 12 ($F_{[2,35]} = 1.57$, $p = 0.04$), suggesting rapid faunal colonization in these experimental plots (Fig. 5).

Polychaetes were the dominant taxonomic group in the bare sediment and vegetated areas (restored and natural meadows), although other groups such as bivalves, gastropods, and malacostraca were also present, particularly in restored and natural meadows (Table 1). Overall, the faunal abundance and taxonomic richness were low (Table 1).

Discussion

This study demonstrates the feasibility of restoring the pioneer narrow leaf *Halodule uninervis* at Inhaca Island, Southern Mozambique, showing that both plug and single shoot methods can be used to restore this important seagrass species. Both planting densities (low and high) showed high growth rate and establishment in the plots, although the high-shoot density treatments proved most effective, resulting in ~1000 shoots/m^2 within a year at both sites tested. Our findings also indicate a rapid benthic macrofauna colonization on the planted sites, with macrofaunal assemblage composition in restoring plots revealing similarities to natural seagrass meadows after 8 months of the transplantation. Benthic macrofauna richness was generally low and primarily dominated by polychaetes, followed by bivalves, malacostraca, and gastropods. These results contribute to strengthening the knowledge of restoration approaches for pioneer seagrass species such as *H. uninervis* in the Western Indian Ocean region, where human-induced threats to seagrasses are increasing (Unsworth & Cullen 2010; UNEP 2020). These results are particularly significant considering the reliance of dugongs on this seagrass species and the potential reversal of its decline due to anthropogenic activities through restoration efforts.

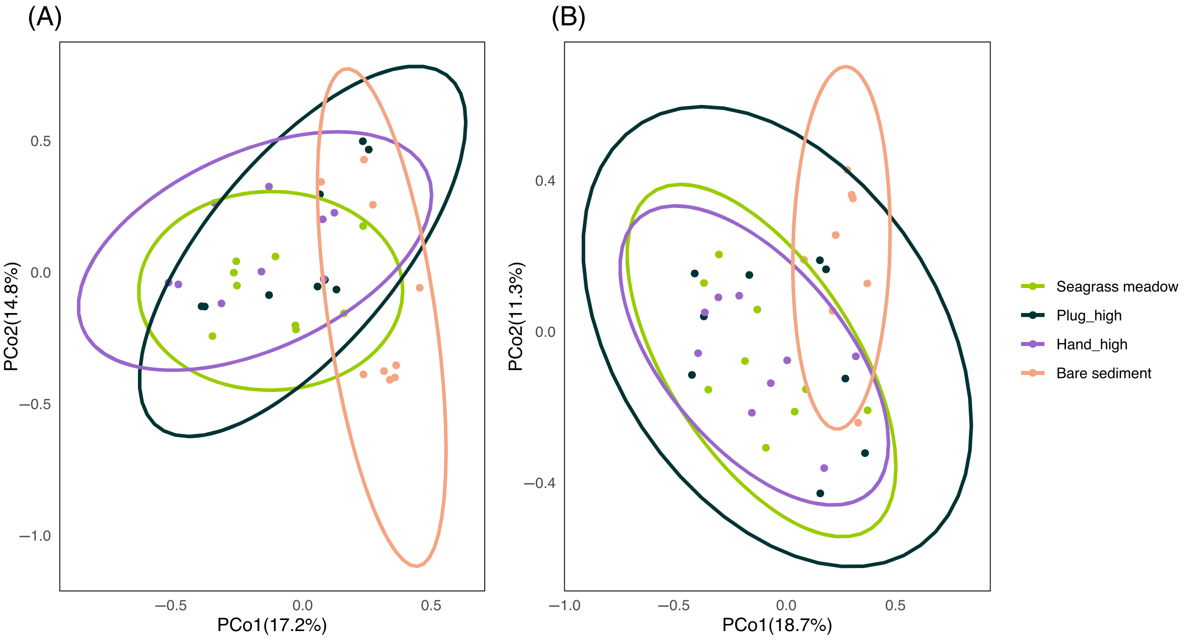

Figure 5. Constrained principal coordinate ordination (PCO), based on fourth-root transformed Bray–Curtis similarity measures, visualizing differences between restoration plots (plug and single shoot methods), the natural meadow, and bare sediment after 8, 10, and 12 months on macrofauna assemblage composition at (A) Bangua and (B) the EBMI site.

Table 1. Macrofauna abundances and richness (based on Shannon–Wiener index) in the experimental plots, the natural meadow, and the bare sediment area after 8, 10, and 12 months in two studied sites (EBMI and Bangua site; Fig. 1). Others are (Holothuridae, Asteroidea, and Ophiuroidea). Values are mean ± SE ($n = 3$).

			Fauna abundance (m^{-2})			
Sites	*Time after planting*	*Plots groups*	*Seagrass meadow*	*Plug-high*	*Shoot-high*	*Bare sediment*
EBMI	8 months	Polychaetes	382 (147)	509 (147)	509 (73)	297 (153)
		Bivalves	127 (73)	85 (42)	127 (74)	0
		Gastropods	85 (85)	0	0	42 (42)
		Malacostraca	212 (85)	42 (42)	212 (42)	85 (42)
		Others	0	85 (85)	127 (73)	0
		Richness	1.4 (0.2)	1.3 (0.2)	1.7 (0.4)	0.9 (0.4)
	10 months	Polychaetes	510 (74)	255 (74)	297 (42)	510 (74)
		Bivalves	42 (42)	85 (42)	170 (112)	85 (42)
		Gastropods	0	42 (42)	0	0
		Malacostraca	42 (42)	42 (42)	85 (42)	85 (42)
		Others	127 (127)	0	0	42 (42)
		Richness	1.4 (0.0)	0.8 (0.2)	1.1 (0.1)	1.0 (0.3)
	12 months	Polychaetes	382 (195)	425 (112)	425 (236)	255 (74)
		Bivalves	127 (0)	0	127 (127)	42 (42)
		Gastropods	85 (42)	0	170 (85)	0
		Malacostraca	42 (42)	0	0	85 (42)
		Others	127 (74)	0	0	42 (42)
		Richness	1.5 (0.2)	0.7 (0.4)	1.4 (0.0)	0.8 (0.5)
Bangua	8 months	Polychaetes	170 (42)	212 (42)	467 (258)	510 (74)
		Bivalves	127 (74)	85 (85)	85 (42)	0
		Gastropods	42 (42)	0	42 (42)	0
		Malacostraca	212 (85)	85 (42)	127 (74)	85 (85)
		Others	42 (42)	0	85 (85)	0
		Richness	1.3 (0.0)	0.9 (0.2)	1.1 (0.4)	1.3 (0.3)
	10 months	Polychaetes	467 (185)	467 (278)	467 (112)	297 (42)
		Bivalves	0	0	0	0
		Gastropods	0	42 (42)	42 (42)	85 (85)
		Malacostraca	127 (127)	0	0	42 (42)
		Others	42 (42)	0	0	0
		Richness	0.7 (0.4)	0.7 (0.4)	1.2 (0.1)	1.0 (0.2)
	12 months	Polychaetes	340 (42)	255 (74)	340 (42)	255 (74)
		Bivalves	85 (42)	42 (42)	0	42 (42)
		Gastropods	42 (42)	42 (42)	42 (42)	0
		Malacostraca	85 (42)	42 (42)	42 (42)	42 (42)
		Others	124 (74)	42 (42)	42 (42)	0
		Richness	1.2 (0.3)	1.0 (0.5)	1.0 (0.2)	0.7 (0.4)

Restoration Methods for *Halodule uninervis*

Our results revealed a higher growth rate (~300–800%) using the plug method and the high-shoot density treatments (~300 shoot/m^2) after 16 months of planting at both tested sites. Similar findings were observed in a previous study using the seagrass *Syringodium isoetifolium* in the coast of Dar es Salaam, Tanzania, in which transplants showed a higher growth rate (33.3–66.7%) using a plug method compared to a single shoot method (Wegoro et al. 2022). Other studies using *Zostera muelleri* in Australia also showed that plants transplanted using plug methods outperformed when compared to bare-rooted transplantation (e.g. Tan et al. 2020, 2023). This success can be explained by the fact that in the plug method, plants are transplanted rooted in their original sediment (Phillips 1990), improving their establishment and survival rate.

Our results showed that the seagrass harvesting method for transplantations did not negatively impact the seagrass shoot density in the donor plots since at EBMI they were two times higher in the donor plots than in the adjacent natural meadows, and in Bangua, the donor plots reached similar densities of natural meadows after 10 months of transplanting, revealing a recovery of donor plots in less than a year.

The high-density treatments (~300 shoot/m^2) using both tested methods contributed to a higher seagrass growth rate compared to low-density treatments. This is in accordance with previous studies (e.g. Van Katwijk et al. 2016; Paulo et al. 2019), showing that the combination of high plant densities and large-scale planting enhances suitable conditions for plant survival and growth.

Planting seagrass seeds or seedlings have been widely attempted in temperate and subtropical regions (e.g. Orth et al. 2012; Eriander et al. 2016; Infantes et al. 2016; Escandell-Westcott et al. 2023; Gräfnings et al. 2023; Tan et al. 2023), showing variable restoration success responses. Here, we used transplants instead of seeds and seedlings, since *H. uninervis* has small seeds with limited dispersal capacity, which might confer this species a negligible sexual recolonization (Olesen et al. 2004). Indeed, seed-based approaches in many tropical countries are still not well developed because the timing, intensity, and frequency of flowering and seed production for most seagrass species require more research (UNEP 2020). However, some studies have shown successful germination (e.g. Tan et al. 2023) and/or seagrass survival (e.g. Orth et al. 2012, 2020) using seeds, which was due to a combination of species traits (e.g. seed yield, seed dispersal, and adequate germination) and favorable site conditions (e.g. water quality and depth).

The results also revealed that sediment conditions seem favorable for the development of *H. uninervis* at both planted sites. Bangua had a lower percent of sedimentary organic matter compared to EBMI; however, in both tested sites, the growth rate of plants was higher than 100% at the end of the experiment. Nonetheless, we observed a variation in shoot density (most noticeable in EBMI) throughout the experiment. This can be related to a seasonal effect, since the reduction in the number of shoots was observed at month 12 (peak of summer), followed by an increase at month 16. This trend was not in accordance with de Boer (2000), who reported high-shoot density of *H. uninervis* (former *H. wrightii*) in summer at Inhaca Island. *Halodule uninervis* in Maputo Bay is characterized by high morphological and physiological plasticity, which might be related to environmental conditions, thus limiting its distribution and variability across the intertidal zone (Muth & Bandeira 2014). Although not clearly assessed, field observations suggest that in specific locations, particularly in areas close to EBMI (one of the planting site), the aboveground parts (shoots and leaves) of *H. uninervis* disappear during certain seasons, while the belowground components (rhizomes and roots) remain consistent. This phenomenon, which requires further investigation, might be associated with heat stress (Bandeira et al. 2014) and could explain the pattern observed during the experiment. This suggests that desiccation stress due to time of exposure and higher mean air and water temperatures, might have exceeded the buffering capacity of seagrass, leading to die-offs (Maxwell et al. 2016).

In addition, field measures were conducted by five persons (two for plug methods and three for single shoots) with the time required for collection and planting of ~2.5 hours using both methods, when the transplanting plots were located close to the donor meadows (~100 m apart). Thus, both methods can be recommended for large-scale restoration, but the cost of transportation and storage of plugs with sediment and seagrass, as well as larger impacts on donor meadows after collection, should be taken into consideration when deciding to use the plug method. Indeed, the plug method is described as more labor-intensive compared to the single method (Fonseca et al. 1998) and has the greatest potential impact on donor meadows as it requires the removal of shoots at high density levels (Tan et al. 2023).

Results also support the development of an appropriate approach to restoring pioneer species, such as *H. uninervis*, which can be used as a baseline for future restoration efforts of slower-growing climax species (see Kenworthy et al. 2018). In Mozambique, most seagrass meadows are formed by a mix of species, comprising up to four species confined in small areas (<1 km) (Bandeira et al. 2014; Cossa et al. 2023). Therefore, this approach can be used to support large restoration initiatives of climax species, while creating less impact in donor beds and enhancing shellfish productivity, which has decreased in the last years, mostly due to digging activity by shellfish harvesters (Chitará-Nhandimo et al. 2022; Mafambissa et al. 2022).

Macrofauna Colonization in Restoring Plots

Monitoring the recovery of biodiversity in planted seagrass meadows is crucial to understanding the effectiveness of restoration approaches and assessing their long-term positive impact on ecosystem functions (Fonseca et al. 1996; McSkimming et al. 2016; Tanner et al. 2021). In this study, we found rapid fauna colonization in restoration plots after 8–12 months, with fauna composition dominated by polychaetes being similar ($p > 0.05$) to adjacent natural meadows at both tested sites. This is in accordance with previous studies showing a quick recovery of faunal assemblages in restored sites due to the provision of structure by seagrass when shoot densities reached similar proportions compared to adjacent natural meadows (e.g. Bell et al. 1993; Tanner et al. 2021; Gagnon et al. 2023).

In this study, planting locations were selected close to the natural meadows where plants could grow since the goal of the study was to assess the efficiency of two planting methods. The proximity of transplanted and reference sites (~100 m) might have affected fauna density and composition since restored sites close to natural meadows have a greater probability of attracting fauna with dispersal stage (Sheridan et al. 2003; McSkimming et al. 2016; Tanner et al. 2021).

The results revealed low species richness and polychaetes were the dominant taxon in the natural meadows, restoration plots, and adjacent bare sediments. Polychaetes are frequently found in soft-bottom sediments, playing an important role in nutrient cycling and for secondary production (Kristensen et al. 2014). For instance, Bell et al. (1993) found that deposit-feeding polychaetes were abundant at both natural and planted seagrass sites in Tampa Bay, Florida. Further, our results also showed higher abundances of other taxonomic groups (bivalves, malocastraca, and gastropods) in seagrass meadows and transplanted sites compared to bare sediments. This finding is in line with the fact that seagrass meadows are known to support higher species richness and abundance of fauna than neighboring non-vegetated habitats (Boström et al. 2006).

This study is the first attempt to assess fauna colonization in *H. uninervis* restored plots at Western Indian Ocean, and so, results might not be representative for other meadows in the area. Firstly, the initial restoration plot size was small (1 m^2), which might result in samples with high fauna density due to an edge effect, although this was not confirmed in this study since the restoration plots expanded over time. Therefore, the composition of infauna (based on the most abundant taxa) in this study appears to be less affected by fragmentation compared to large, motile fauna, as shown also by Boström et al. (2006). However, the relationship between structural complexity (patch size and shoot density) and fauna abundance in restoration sites remains controversial, with some studies showing no relation, while others showed significant correlations (see Fonseca et al. 1996; Gagnon et al. 2023). Second, fauna samples were taken during low tide, which might have affected our fauna results since motile epifauna are likely to show an orientation, dispersing between intertidal and subtidal areas via tidally induced water currents (Tanner 2003). Other experimental designs, including visual surveys and/or drop nets, would be required to fully assess fish and other highly motile macrofauna. Regardless, this study corroborates that fauna assemblages have the potential to quickly colonize restored seagrass meadows at Inhaca Island. However, long-term experiments are needed to better assess the fauna assemblages in restoring sites while exploring the factors that might influence their colonization.

Restoring *Halodule uninervis*: A Management Tool?

Loss of seagrasses can have profound ecological and socioeconomic impacts, such as decreasing carbon sequestration and nutrient cycling, and threatening many seagrass-dependent species (Waycott et al. 2009; Short et al. 2011; Moksnes et al. 2021), such as dugongs, which are listed by World Conservation Union as vulnerable species.

In the Western Indian Ocean, invertebrate harvesting on seagrass has been attributed as one of the main causes of impact on seagrass, affecting their ecosystem services (Nordlund et al. 2010; Unsworth & Cullen 2010). Therefore, managing seagrass meadows requires an effective approach, which includes developing restoration initiatives to offset the loss of their ecosystem functions and services. Here, we tested the efficiency of restoration techniques on *H. uninervis*, a preferred food source for dugongs at Inhaca Island (Fernando et al. 2014; Cossa et al. 2023). *Halodule uninervis* has shown rapid colonization and recovery; however, the importance of adopting approaches to identify areas for effective conservation and/or restoration efforts is critical due to increasing anthropogenic (e.g. use of destructive fishing gears) and natural impacts (e.g. cyclones) on seagrass in the area (Bandeira et al. 2021; Chitará-Nhandimo et al. 2022; Amone-Mabuto et al. 2023).

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Supporting Information

The following information may be found in the online version of this article:

Table S1. Three-way ANOVA of average proportional shoot density differences from months 0 to 16.

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