Recovery of a Halodule wrightii donor meadow

Article *in* Restoration Ecology · October 2023

DOI: 10.1111/rec.14042

4 authors:

Eduardo Gabriel Torres-Conde
Universidad Nacional Autónoma de México

Mariana Alvarez Rocha
Universidad Nacional Autónoma de México

Roberto Lindig Cisneros
Universidad Nacional Autónoma de México

Brigitta I. van Tussenbroek
Universidad Nacional Autónoma de México

RESTORATION ECOLOGY
The Journal of the Society for Ecological Restoration

RESEARCH ARTICLE

Recovery of a *Halodule wrightii* donor meadow

Eduardo Gabriel Torres-Conde[1,2,3], Mariana Alvarez-Rocha[1], Roberto Lindig-Cisneros[4], Brigitta I. van Tussenbroek[1]

Few restoration studies have quantified the recovery of the donor meadow. We evaluated the recovery of a monospecific donor meadow of *Halodule wrightii*, the second most commonly used transplanting species, and assessed the possible effect of 24 plots of 1 m^2 placed in an approximately 3,400 m^2 large monospecific meadow with a mean cover of 45%, foliar shoot density of 1,280 shoots/m^2, and 16 cm canopy height. Extraction densities were 9, 25, 64, and 121 small-sized extraction cores (4.5 cm diameter, 20 cm depth), with control and procedural control without extractions ($N = 4$ per treatment). After 6 months, even the plots with the highest extraction densities recovered, as indicated by the shoot number in the extraction areas and seagrass cover in the plots approaching the levels in the controls. The recovery occurred under the environmental conditions: light availability (22,000 ± 51 lx), relatively stable sediments (0.8–1.16 cm) with a fine sandy composition (mean grain diameter, D50: 0.5 ± 0.22 mm), and low organic matter (0.22 ± 0.012%). The recolonization rate was 1–3 shoots per month in the 4.5 cm diameter extraction areas, independent of the extraction level. Thus, approximately 20% of the *H. wrightii* meadow (corresponding with 121 cores/m^2) could be extracted in our study area. This high extraction intensity can be attributed to the adequate selection of donor species, meadow, and size of the planting unit.

Key words: core transplants, extraction density, recolonization, seagrass restoration, sediments

Implications for Practice

- For the selection of seagrass donor meadows, if possible, select a donor species with high rhizome elongation rates, allowing for fast recovery.
- Consider opting for a donor site with a large vegetation area to maintain positive feedback processes.
- Consider the selection of a donor site with as optimal environmental conditions as possible.
- Take into consideration the use of the smallest-sized core extraction to obtain a viable planting unit.

Introduction

Transplanting vegetative plant material from donor meadows to damaged areas has been among the most widely used methods for seagrass restoration (Fonseca et al. 1998; Paling et al. 2009; Pereda-Briones et al. 2018). However, the impact of the extraction of seagrass plants from the donor meadows has been understudied, even though various works have emphasized that information on the recovery of donor meadows is essential in deciding whether the removal of plant material is sustainable (Short & Wyllie-Echeverría 1996; Paling et al. 2009; van Katwijk et al. 2009). van Katwijk et al. (2016) reported that only 15% of the restoration studies using transplants mentioned the state of the donor meadow after extractions. Few published articles have quantified the recovery (Table 1), and even less is known concerning suitable harvesting/extraction densities. This constitutes a gap in the knowledge of seagrass restoration.

From a donor meadow perspective, it is better to use faster-growing species (having higher rhizome extension rates) if more seagrass species are available, as the donor meadow of such species is likely to recover faster (Marbá et al. 2004; Uhrin et al. 2009). In addition, faster-growing species may be more suitable for transplants as they tend to have a higher tolerance to different environmental conditions than species with lower rhizome elongation rates (Burkholder et al. 1994; Fonseca et al. 1994; Marbá & Duarte 1998). Transplant host sites usually have difficult conditions for transplant establishment, such as

Author contributions: EGTC, BIVT, RLC conceived and designed the research; EGTC, MAR, BIVT performed the experiments; EGTC, BIVT, MAR, RLC wrote and edited the manuscript.

[1]Unidad Académica de Sistemas Arrecifales-Puerto Morelos, Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, Puerto Morelos, Quintana Roo, Mexico
[2]Unidad de Posgrado, Edificio D, 1° Piso, Circuito de Posgrados, Ciudad Universitaria, Coyoacán, C.P. 04510, Distrito Federal, México
[3]Address correspondence to E. G. Torres-Conde, email etorresconde2@gmail.com
[4]Instituto de Investigaciones en Ecosistemas y Sustentabilidad. Universidad Nacional Autónoma de México (UNAM), Antigua Carretera Pátzcuaro No. 8701, Sin Nombre, Morelia, Michoacán, Mexico

doi: 10.1111/rec.14042
Supporting information at:
http://onlinelibrary.wiley.com/doi/10.1111/rec.14042/suppinfo

Table 1. Studies of the recovery of seagrass donor meadows. PU, planting unit; PU size in cm^2 (if an area of the mat is extracted) or cm (length of rhizome section); NA, not available; *H. wrightii*, *Halodule wrightii*; *S. filiforme*, *Syringodium filiforme*; *P. sinuosa*, *Posidonia sinuosa*; *P. australis*, *Posidonia australis*; *Z. noltei*, *Zostera noltei*; *Z. muelleri*, *Zostera muelleri*; *Z. marina*, *Zostera marina*. The rhizome excavations were all realized by hand. All meadows fully recovered. Rhizome elongation rates were obtained from Marbá and Duarte (1998), and Turner et al. (1996) for *Z. muelleri*. [a]Rhizomes collected in the center of the meadow. [b]Rhizomes collected at the edge of the meadow.

Species	*Rhizome elongation rate (cm/yr)*	*Location*	*Harvesting technique*	*PU size*	*No. PU*	*Total extracted area (m^2)*	*Donor meadow size (m^2)*	*Recovery time (months)*	*Source*
H. wrightii	81–365	USA	Rhizome excavation	100, 630, 2,500 cm^2	12	1.29	NA	~12	Fonseca et al. (1994)
S. filiforme	52–182	USA	Rhizome excavation	100, 630, 2,500 cm^2	12	1.29	NA	~12	Fonseca et al. (1994)
Z. noltei	10–127	Spain	Sods	1,026 cm^2	17	1.74	NA	12	Valle et al. (2015)
Z. muelleri	77–97	New Zealand	Mats	10 cm^2	25	1.5	1,440	9	Matheson et al. (2017)
Z. muelleri	77–97	New Zealand	Rhizome excavation	10 cm^2	25	1.5	1,440	9	Matheson et al. (2017)
Z. muelleri	77–97	New Zealand	Sods	10 cm^2	25	1.5	1,440	9	Matheson et al. (2017)
Z. marina	22–31	USA	Rhizome excavation	3–5 cm	250×10^3	NA	60,000	~12	Davis and Short (1997)
Z. marina	22–31	China	Rhizome excavation[a]	100–2,500 cm^2	40	4.4	2,000,000	~7	Zhang et al. (2021)
Z. marina	22–31	China	Rhizome excavation[b]	100–1,600 cm^2		2.4	2,000,000	~12	Zhang et al. (2021)
P. australis	9–10	Australia	Cores	8.3 cm		NA	NA	~48	Verduin et al. (2012)
P. sinuosa	2–6	Australia	Cores	8.3 cm		NA	NA	~48	Verduin et al. (2012)

poor sediment stability, high turbidity, or poor light penetration due to the losses of seagrasses (van Katwijk et al. 2009, 2016).

Vegetative transplants can be obtained by several means, such as beached plant sections (Terrados et al. 2013), uprooted shoots (Zhou et al. 2014), cultivated plants from a land-based nursery (Tanner & Parham 2010), or harvesting wild plants from donor meadows (Paulo et al. 2019). The first three methods do not involve extraction from a donor meadow. The fourth method can damage the donor meadow and, in addition, generate changes in local sediment dynamics with erosive impacts, which may impair or delay the recolonization (Maxwell et al. 2017; Githaiga et al. 2019). Plants can be extracted from a donor meadow with or without sediments, but the introduction of transplants with the original sediments preserves the rooting environment and provides better anchorage, resulting in successful transplant establishment (Paling et al. 2001; Hall et al. 2006; McDonald et al. 2020). Paulo et al. (2019) comment that the failure rate of using sediment-free methods has been high (e.g., 100% failure for *Zostera marina*, *Zostera noltei*, and *Cymodocea nodosa* in Portugal) and recommend using seagrass harvesting methods with their natural sediment. Sods and cores/plugs are the most common and effective extraction methods with sediments, but small-sized cores are preferred if the damage to the donor meadow should be minimized (Verduin et al. 2012; Paulo et al. 2019; McDonald et al. 2020).

For the selection of the donor meadow, the following guidelines have been recommended; however, for logistic reasons, it is often not possible to follow all: (1) proximity to the transplant site; (2) large vegetation area; (3) suitable environmental conditions; and (4) sufficient genetic variation (Fonseca et al. 1998; van Katwijk et al. 2009; Cunha et al. 2012). A donor meadow close to the transplant site increases the presence of locally adapted gene complexes (Sinclair et al. 2013; van Katwijk et al. 2016). This also favors a plant material with a better physiological state for planting and a lower investment cost as transport times and distances are short (van Katwijk et al. 2009, 2016). A meadow with a large vegetation area could provide sufficient plant material for harvesting and diminish the impact of the extractions. A large donor meadow could also favor the recovery through seagrass-positive feedback processes, which are density-depending auto-facilitation processes (e.g., roots stabilizing sediments for better establishment of new shoots) (van Katwijk et al. 2009; Maxwell et al. 2017). Likewise, a donor site with a habitat with sufficient light and appropriate sediments (e.g., fine sandy, stable, low organic matter load) has suitable environmental conditions for meadow recovery (van Katwijk et al. 2009; Valle et al. 2015; van Katwijk et al. 2016). Plants from a genetically variable meadow are preferred, as they are thought to adapt to environmental changes and avoid inbreeding, but such studies are costly (van Katwijk et al. 2009).

This study analyzes the recovery of a donor meadow of *Halodule wrightii* in relation to the extraction density of small cores in a Mexican Caribbean reef lagoon. We test the hypothesis that the higher the extraction density, the recolonization rate would be reduced. *H. wrightii* is the second most used seagrass species in restoration efforts (58 trials) after *Z. marina* (202) (van Katwijk et al. 2016). *H. wrightii* is a faster-growing species (horizontal rhizome extension rate of 80–365 cm/year; Marbá & Duarte 1998) and is tolerant to low light conditions due to water turbidity (14–33% surface irradiance) and variable salinity conditions (15–30) and can persist in unstable and disturbed environments (Larkin et al. 2008; McDonald et al. 2020).

Methods

Study Area

The Puerto Morelos reef lagoon, in the Mexican Caribbean, stretches from the coastline to the coral reef, ranging from approximately 350–3,100 m with a maximal depth of 3–4 m (8 m in navigation channels). The lagoon has well-developed seagrass meadows, composed of *Thalassia testudinum* and *Syringodium filiforme*, *Halodule wrigthii*, and rhizophytic algae (van Tussenbroek 2011). The studied monospecific *Halodule wrightii* donor meadow (20°59.431′N, 86°49.272′O) was approximately 700 m from the shoreline and approximately 1 km from the nearshore target area for restoration. The meadow was in the area of marine sand waves or dunes (Fig. 1A) and had an area of approximately 3,400 m^2 and an average depth of 2.5 m.

Characterization of the Donor Meadow

H. wrightii foliar shoot density, percent cover, and canopy height (mm) were measured by randomly placing 13 quadrats of 0.25 m^2. For each quadrat, the foliar shoots (i.e., leaf-bearing shoots) were counted, and their density (no. foliar shoots/m^2) was determined. Percent cover was visually estimated, and the lengths of the 10 longest leaves of haphazardly selected foliar shoots were measured with a ruler, and the mean was considered as a proxy of canopy height (cm).

Four sediment surface samples (approximately 400 g wet) were randomly taken by scoops. In the laboratory, large particles were removed (e.g., shells, rocks, plant material), and the samples were placed in a drying oven for 48 hours at 60°C. For granulometric analysis, 120–200 g of sediment was separated from each sample and was processed with a Camsizer-L Retsch Technology particle analyzer to obtain the sediment grain size distribution, including mean grain diameter (D50). Forty replicates were performed per sample. For organic matter analysis, 2 g of sediment was separated, and % organic matter was determined following the standard procedure of loss-on-ignition of Heiri et al. (2001). Five replicates were performed per sample.

To measure luminance (lux), a logger (model UA-002-08, HOBO; Onset Computer Corp.; Bourne, MA, USA) was placed 3 cm above the donor meadow canopy. The HOBO was calibrated to capture data every 15 min. Data from daylight peaks (between 10 and 13 h) for 3 months were used.

Experimental Design

Twenty-four 1 m^2 (1 × 1 m) plots were established in the interior of the donor bed by SCUBA diving at a minimal distance of 2 m from one another. The plots were delimited with metal rods and nylon string. Six treatments, consisting of distinct

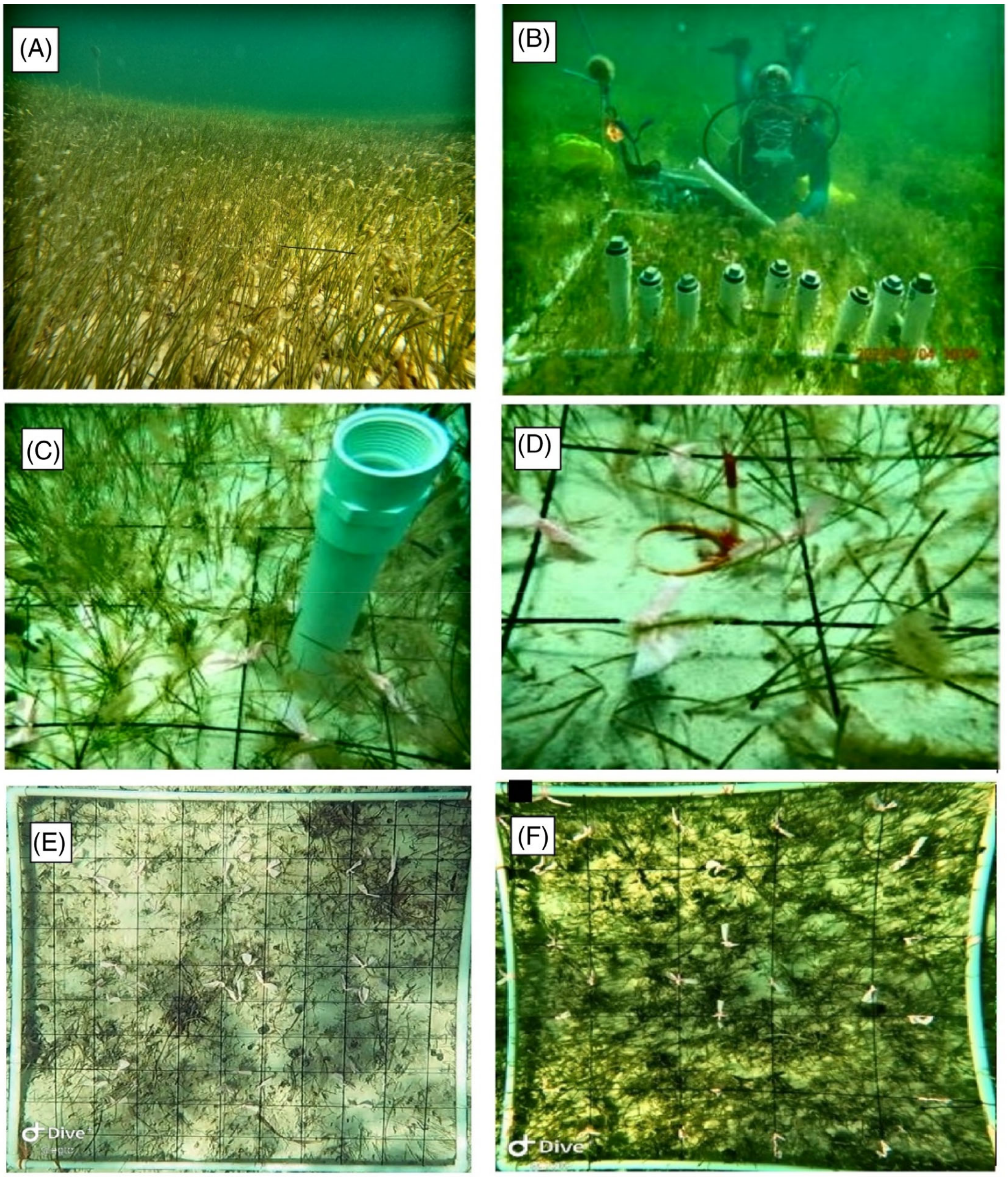

Figure 1. (A) Donor meadow of the seagrass *Halodule wrightii*; (B) coring in process for 121 extractions; (C) close-up image of a core inserted in the seagrass meadow; (D) placement of the circular frame where a core was extracted, indicating the extraction area; (E) plot of *H. wrightii* after the extraction of 121 cores; (F) cover in the same plot after 6 months.

levels of extraction (expressed as the number of extracted cores per plot), a procedural control, and control, were assigned randomly to the numbered plots, with four replicates per treatment. The extraction treatment had four levels of 9, 25, 64, and 121 cores (see below) per plot; the procedural control consisted of nine insertions of the corer without removing the seagrasses, and the control had no manipulation (Table 2). The cores were extracted following a regular spacing pattern in grids. The grids were established by spanning cords equally spaced across the quadrants; the number of cords depended on the extraction treatment (Table 2; Fig. 1). In total, 876 cores were extracted.

Core Extractions

H. wrightii was extracted using 40-cm long PVC corers with a diameter of 4.5 cm (Fig. 1B & 1C). The cores were buried 20 cm, taking sediment and *H. wrightii* (between 3 and 10 foliar shoots per core), and two caps were placed on the extremes of them to allow for transport to the target site for restoration. The sediments consisted of loose sand, and it was not necessary to backfill the holes generated by the cores because the fine sandy sediments quickly filled them without intervention. The cores were inserted in the same manner for the procedural control, but no *H. wrightii* foliar shoots or sediment was extracted.

Table 2. Extraction treatments and levels (number of 4.5 diameter core extractions) of *Halodule wrightii*. The procedural control consisted of nine insertions of the cores without extraction, and the control did not receive any manipulation. The plot area was 1 m^2, and there were four plots per treatment.

Extraction treatments	*Level (no. extractions)*	*Extracted area per plot (cm^2)*	*% of area extracted*
Control	0	0	0
Proc. control	0	0	0
Minimal density	9	143.1	1.4
Low density	25	397.6	4.0
High density	64	1,017.9	10.2
Maximal density	121	1924.4	19.2

Nine extraction areas per plot were marked (in the same approximate position per plot), immediately after removal of the core, using 25 cm tall wooden stakes with attached circular frames (diameter 4.5 cm), that indicated the precise location of the areas of extraction. The wooden stakes were buried 18 cm, leaving 7 cm above the sediment (Fig. 1D). Extractions were made during the second half of July 2022 and were completed on 25 July, which was considered as the starting date of the observations on recovery.

Monitoring the Recovery

Monthly or bimonthly (every 2 months) surveys were conducted to observe the recovery of the *H. wrightii* donor meadow from July 2022 to January 2023. The foliar shoots were counted in the nine circular frames per plot that marked the precise location of core extraction. The cover of *H. wrightii* in the plots was determined by placing a 1 m^2 square frame with 0.2 m^2 subdivisions as a guide. Five photographs covering the 0.2 m^2 areas arranged diagonally in the plot were taken with a GoPro 9 camera. The cover percent in each photo was estimated with a 10×10 grid. In addition, the lengths of the wooden stakes above the sediment were measured with a ruler (0.1 mm accuracy) to estimate changes in sediment level.

Statistical Analysis

The mean number of foliar shoots, in the marked nine extraction areas per plot, was determined and an increase in number was considered as recolonization. A *t*-Student test was performed for the number of foliar shoots after 1 month, between the control and the procedural control, to test for a possible effect of the core manipulation on the number of foliar shoots. Since differences were not statistically significant ($t = 0.505$, $df = 6$, $p = 0.183$), the procedural controls were not further considered in the analyses. The recovery at the meadow level was expressed as changes in the percent of the mean cover of *H. wrightii* per plot. Changes in the sediment levels were defined as the mean difference in the lengths of the nine stakes (per plot) between the observed time and those measured in the previous months (or 2 months).

Possible differences in the recovery of *H. wrightii* among treatments and time were tested with repeated measures ANOVA with a number of foliar shoots in extracted areas and cover of *H. wrightti* in the plots as response variables and treatments and months as factors. The post hoc SNK (Student–Newman–Keuls) test was used to compare pairs of means. The same analysis was applied to determine possible differences in sediment levels among treatments and time. A significance level of 0.05 was used for all tests. All analyses were done in R (R Core Team 2023) using packages: ggpubr (Kassambara 2020) and GAD (Sandrini-Neto & Camargo 2012). The data complied with the assumptions of homogeneity of variances (Levene test) and normality (Shapiro–Wilk test).

Results

Characterization of the Donor Meadow

At the beginning of the experiment, the meadow had a mean (± standard error) coverage of 45 ± 5.2% ($N = 13$), foliar shoot density of 1,280 ± 102.2 shoots/m^2 ($N = 13$), and canopy height of 16 ± 1.5 cm ($N = 13$). The sediments presented a fine and sandy composition (D50: 0.5 ± 0.22 mm, $N = 40$) (Fig. S1), with an organic matter content of 0.22 ± 0.012% ($N = 5$). The irradiation at canopy level was 22,000 ± 51 lx ($N = 1,440$) between 10 and 13 h from 10 January 2023 to 10 March 2023.

Recolonization of the Extraction Areas

The number of foliar shoots increased significantly in the extraction areas over time ($F = 104.20$, $df = 5$, $p < 0.001$), independently of the extraction density ($F = 1.45$, $df = 3$, $p = 0.099$; Fig. 2A), approaching those in the controls after 6 months. Most plots showed a mean increment of 1–3 shoots per month in the 4.5-cm diameter extraction areas.

Cover of *Halodule wrightii*

Overall, the cover in the plots increased significantly over time ($F = 45.82$, $df = 5$, $p < 0.001$) and varied significantly among the levels of extraction density ($F = 78.58$, $df = 4$, $p < 0.001$). The plots with 0 (control), 9, and 25 extractions always displayed a similar cover. In the beginning, the cover in the plots where 64 and 121 cores were extracted was significantly lower than those in the controls, showing an initial 22% and 30% cover losses, respectively (Fig. 1E). In the following months, cover increased in these plots by 6.1 and 7.1% per month, respectively. The cover in these plots with the

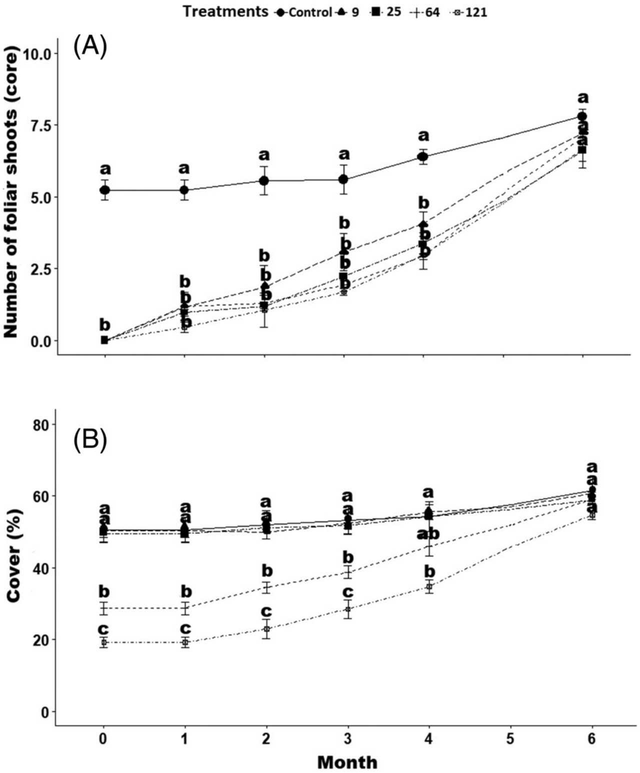

Figure 2. (A) Number of *Halodule wrightii* foliar shoots (mean ± SE) per core area (diameter 4.5 cm), and (B) percent cover in five treatments with different numbers of extraction cores over a 6-month monitoring period on a donor seagrass meadow. The number of replicas per treatment was 4. Different letters indicate significant differences between treatments per month using the Student–Newman–Keuls test at the 0.05 significance level.

highest extraction densities approached the cover in the control plots after 6 months (Figs. 1F & 2B).

Sediment Levels

The sediment levels did not vary over time during the observation period ($F = 1.21$, $df = 5$, $p = 0.092$), independently of the extraction density level ($F = 0.47$, $df = 4$, $p = 0.591$). The plots showed a mean increment in sediment level of 0.8–1.16 cm during the study period.

Discussion

The *Halodule wrightii* donor meadow recovered its seagrass cover 6 months after the core extractions, and the recolonization rate of the extracted areas was independent of the density of the core extractions. The recovery period was shorter than that registered for the same species in the U.S.A. (approximately 12 months; Fonseca et al. 1994). Other seagrass species with somewhat lower rhizome elongation rates, such as *Syringodium filiforme* (Fonseca et al. 1994), *Zostera noltei* (Valle et al. 2015), *Zostera muelleri* (Matheson et al. 2017), and *Zostera marina* (Davis & Short 1997; Zhang et al. 2021) recovered between 9 (exceptionally 7) and 12 months. Species with low rhizome elongation rates, such as *Posidonia australis* and *Posidonia sinuosa* needed 3–4 years to fully colonize a small extraction area of 26 cm^2 (Verduin et al. 2012). Thus, the selection of donor meadows of species with high to medium rhizome elongation rates could be adequate for sustainable extractions and rapid recovery (≤1 year). The highest extraction density of 121 cores, corresponding with the extraction of almost 20% of the *H. wrightii* donor meadow, did not approach a critical threshold for its collapse (Carr et al. 2010). Often, seagrasses present a slowdown in their recovery after disturbance when approaching this critical threshold (critical slowing down) (El-Hacen et al. 2018). *H. wrightii*, even in the plots with the highest extraction density, showed a similar recovery trajectory (approximately 1–3 shoots per month) as the lower extraction density levels.

H. wrightii has the highest horizontal rhizome extension rate among Mexican Caribbean seagrass species (220 cm/year; Gallegos et al. 1994) and is known to recover rapidly after low to moderate disturbances (Larkin et al. 2008). High light availability, typical of the reef lagoon (Naumann et al. 2013), reduced self-shading (due to low canopy height), and relatively stable and fine sands likely favored fast regrowth. Probably the size of the donor meadow (approximately 3,400 m^2) maintained favorable environmental conditions for self-facilitating recovery through positive feedback processes (e.g., abundant rhizome and roots to stabilize the sandy sediments and foliar shoots to attenuate waves and trap resuspended particles increasing light availability).

The position of the extraction points within a meadow may also be of relevance; in this study, the plots were established in the center of the *H. wrightii* meadow. Zhang et al. (2021) reported faster recolonization in extraction areas in the interior of the donor meadow than at its edge. However, this may be context-dependent as other authors found that rhizome growth rates on the edge of the seagrass meadows were higher than in the interior, as seagrasses inside are denser and can affect shoot growth by self-shading and space competition (Marbà et al. 1996; Greve et al. 2005). Furthermore, the use of small-sized cores (4.5-cm diameter) for extraction also likely facilitated the rapid recovery of *H. wrigthtii*, as the smaller the extraction patch size, the faster recovery due to the increase in the area/edge ratio, favoring the expansion of neighboring rhizomes into the bare area (El-Hacen et al. 2018). This is consistent with Zhang et al. (2021), who reported fast recolonization in small extraction units (≤0.25 m^2) of *Z. marina*, promoting shoot production in the donor meadow. The core size must be adequate to extract a viable planting unit, which likely depends on the size of the seagrass species. However, Verduin et al. (2012) already advocated for small-sized core extraction (8.3 cm), even for larger (and slower-growing) species such as *Posidonia oceanica* and *P. australis*.

This study provides evidence that up to 20% of a stable *H. wrightii* meadow under the study's environmental conditions can be extracted using small cores (4.5-cm diameter) for obtaining plant material from the donor meadow without affecting its capacity for recovery. As *H. wrightii* is the second most widely used seagrass species for coastal zone restoration (van Katwijk et al. 2016), this study provides useful information for future efforts.

Acknowledgments

This paper is part of the requirements of the first author for obtaining a Doctoral degree at the Posgrado de Ciencias Biológicas, UNAM. The first author thanks Consejo Nacional de Humanidades, Ciencias y Tecnologías (CONAHCYT) for the graduate scholarship during his studies. We thank the Hotel Moon Palace staff for their support; Edgar Escalante, Miguel Gómez Reali, Guadalupe Barba-Santos, Evelyn Raquel Salas Acosta, and Silvia Valery Ávila Mosqueda of the Unidad Académica de Sistemas Arrecifales-Puerto Morelos for technical support; and Instituto de Ingeniería de la UNAM, for the grain analysis of the sediments. The study received financial support from DGAPA (Dirección General de Asuntos del Personal Académico, UNAM, Project No. PAPIIT AG100321).

LITERATURE CITED

Burkholder JM, Glasgow HB, Cooke JE (1994) Comparative effects of water-column nitrate enrichment on eelgrass *Zostera marina*, shoalgrass *Halodule wrightii*, and widgeongrass *Ruppia maritima*. Marine Ecology Progress Series 105:121–138. https://doi.org/10.3354/meps105121

Carr JD, D'Odorico P, Wiberg P (2010) Stability and bistability of seagrass ecosystems in shallow coastal lagoons: role of feedbacks with sediment resuspension and light attenuation. Journal of Geophysical Research: Biogeosciences 115:1–14. https://doi.org/10.1029/2009JG001103

Cunha AH, Marbá NN, van Katwijk MM, Pickerell C, Henriques M, Bernard G, Ferreira MA, Garcia S, Garmendia JM, Manent P (2012) Changing paradigms in seagrass restoration. Restoration Ecology 20:427–430. https://doi.org/10.1111/j.1526-100X.2012.00878.x

Davis RC, Short FT (1997) Restoring eelgrass, *Zostera marina* L., habitat using a new transplanting technique: the horizontal rhizome method. Aquatic Botany 59:1–15. https://doi.org/10.1016/S0304-3770(97)00034-X

El-Hacen M, Bouma TJ, Fivash GS, Sall AA, Piersma T, Olff H, Govers LL (2018) Evidence for critical slowing down in seagrass: a stress gradient experiment at the southern limit of its range. Scientific Reports 8:17263. https://doi.org/10.1038/s41598-018-34977-5

Fonseca MS, Kenworthy WJ, Courtney FX, Hall MO (1994) Seagrass planting in the southeastern United States: methods for accelerating habitat development. Restoration Ecology 2:198–212. https://doi.org/10.1111/j.1526-100X.1994.tb00067.x

Fonseca MS, Kenworthy WJ, Thayer GW (1998) Guidelines for the conservation and restoration of seagrasses in the United States an adjacent waters. NOAA Coastal Ocean Office, Silver Spring, MD, USA

Gallegos M, Merino M, Rodríguez A, Marbà N, Duarte CM (1994) Growth patterns demography of pioneer Caribbean seagrass *Halodule wrightii* and *Syringodium filiforme*. Marine Ecology Progress Series 109:99–104. https://doi.org/10.3354/meps109099

Githaiga MN, Frouws AM, Kairo JG, Huxham M (2019) Seagrass removal leads to rapid changes in fauna and loss of carbon. Frontiers in Ecology and Evolution 7:62. https://doi.org/10.3389/fevo.2019.00062

Greve TM, Krause-Jensen D, Rasmussen MB, Christensen PB (2005) Means of rapid eelgrass (*Zostera marina* L.) recolonization in former dieback areas. Aquatic Botany 82:143–156. https://doi.org/10.1016/j.aquabot.2005.03.004

Hall LM, Hanisak MD, Virnstein RV (2006) Fragments of the seagrasses *Halodule wrightii* and *Halophila johnsonii* as potential recruits in Indian River Lagoon, Florida. Marine Ecology Progress Series 310:109–117. https://doi.org/10.3354/meps310109

Heiri O, Lotter AF, Lemeke G (2001) Loss on ignition as a method for estimating organic and carbonate content in sediments: reproducibility and comparability of results. Journal of Paleolimnology 25:101–110. https://doi.org/10.1023/A:1008119611481

Kassambara A (2020) Ggpubr: 'ggplot2' based publication ready plots. https://cran.r-project.org/web/packages/ggpubr/index.html (accessed 10 Feb 2023)

Larkin PD, Heideman KL, Parker JE, Hardegree B (2008) Genetic structure of *Halodule wrightii* population from the Laguna Madre Region in the Western Gulf of Mexico. Gulf of Mexico Science 26:124–129. https://doi.org/10.18785/GOMS.2602.04

Marbà N, Cebrián J, Enríquez S, Duarte CM (1996) Growth patterns of Western Mediterranean seagrasses: species-specific responses to seasonal forcing. Marine Ecology Progress Series 133:203–215. https://doi.org/10.3354/meps133203

Marbá N, Duarte CM (1998) Rhizome elongation and seagrass clonal growth. Marine Ecology Progress Series 174:269–280. https://doi.org/10.3354/meps174269

Marbá N, Duarte CM, Alexandre A, Cabaco S (2004) How do seagrasses grow and spread? Pages 11–18. In: Borum J, Duarte C, Krause-Jensen D, Greve T (eds) European seagrasses: an introduction to monitoring and management. The M&MS Project, Copenhagen

Matheson FE, Reed J, Dos Santos VM, Mackay G, Cummings VJ (2017) Seagrass rehabilitation: successful transplants and evaluation of methods at different spatial scales. New Zeland Journal of Marine and Freshwater Research 51:96–109. https://doi.org/10.1080/00288330.2016.1265993

Maxwell PS, Eklof JS, van Katwijk MM, O'Brien KR, de la Torre-Castro M, Bostrom C, Bouma TJ, Krause-Jensen D, Unsworth RKF (2017) The fundamental role of ecological feedback mechanisms for the adaptive management of seagrass ecosystems—a review. Biological Reviews 92: 1521–1538. https://doi.org/10.1111/brc.12294

McDonald AM, Christiaen B, Major KM, Cebrian J (2020) The influence of seagrass donor source on small-scale transplant resilience. Aquatic Conservation: Marine and Freshwater Ecosystems 30:730–742. https://doi.org/10.1002/aqc.3283

Naumann MS, Jantzen C, Haas AF, Iglesias-Prieto R, Wild C (2013) Benthic primary production budget of a Caribbean reef lagoon (Puerto Morelos, Mexico). PLoS One 8:e82923. https://doi.org/10.1371/journal.pone.0082923

Paling EI, Fonseca M, van Katwijk MM, van Keulen M (2009) Seagrass restoration. Pages 687–713. In: Perillo G, Wolanski E, Cahoon D, Brinson M (eds) Coastal Westlands: an integrated ecosystem. Elsevier, Amsterdam

Paling EI, van Keulen M, Wheeler K, Philips J, Dyberg R (2001) Mechanical seagrass transplantation in Western Australia. Ecological Engineering 16: 331–339. https://doi.org/10.1016/S0925-8574(00)00119-1

Paulo D, Cunha AH, Boavida J, Serrao EA, Goncalves EJ, Fonseca M (2019) Open coast seagrass restoration. Can we do it? Large scale seagrass transplants. Frontiers in Marine Science 6:52. https://doi.org/10.3389/fmars.2019.00052

Pereda-Briones L, Tomas F, Terrados J (2018) Field transplantation of seagrass (*Posidonia oceanica*), seedlings: effects of invasive algae and nutrients. Marine Pollution Bulletin 134:160–165. https://doi.org/10.1016/j.marpolbul.2017.09.034

R Core Team (2023) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria https://www.R-project.org

Sandrini-Neto L, Camargo MG (2012) GAD based publication ready plots. https://cran.r-project.org/web/packages/GAD/index.html (accessed 10 Feb 2023)

Short FT, Wyllie-Echeverría S (1996) Natural and human-induced disturbance of seagrasses. Environmental Conservation 23:17–27. https://doi.org/10.1017/S0376892900038212

Sinclair EA, Verduin JJ, Krauss SL, Hardinge J, Anthony J, Kendrick GA (2013) A genetic assessment of a successful seagrass meadow (*Posidonia australis*) restoration trial. Ecological Management and Restoration 14:68–71. https://doi.org/10.1111/emr.12028

Tanner CE, Parham T (2010) Growing *Zostera marina* (eelgrass) from seeds in land-based culture systems for use in restoration projects. Restoration Ecology 18:527–537. https://doi.org/10.1111/j.1526-100X.2010.00693.x

Terrados J, Marín A, Celdrán D (2013) Use of *Posidonia oceanica* seedlings from beach-cast fruits for seagrass planting. Botanica Marina 56:185–195. https://doi.org/10.1515/bot-2012-0200

Turner SJ, Thrush SF, Wilkinson MR, Hewitt JE, Cummings VJ, Schwarz A-M, Morrisey DJ, Hawes I (1996) Patch dynamics of the seagrass *Zostera novazelandica* at three sites in New Zealand. Pages 21–31. In: Kuo J, Walker DI, Kirkman H (eds) Seagrass biology: scientific discussion from an international workshop. The University of Western Australia, Perth

Uhrin AV, Hall MO, Merello MF, Fonseca MS (2009) Survival and expansion of mechanically transplanted seagrass sods. Restoration Ecology 17:359–368. https://doi.org/10.1111/j.1526-100X.2008.00376.x

Valle M, Garmendia JM, Chust G, Franco J, Borja A (2015) Increasing the chance of successful restoration of *Zostera noltii* meadows. Aquatic Botany 127:12–19. https://doi.org/10.1016/j.aquabot.2015.07.002

van Katwijk MM, Bos AR, de Jonge VN, Hanssen LSAM, Hermus DCR, de Jong DJ (2009) Guidelines for seagrass restoration: importance of habitat selection and donor population, spreading of risks, and ecosystem engineering effects. Marine Pollution Bulletin 58:179–188. https://doi.org/10.1016/j.marpolbul.2008.09.028

van Katwijk MM, Thorhaug A, Marbá N, Orth RJ, Duarte CM, Kendrick GA, et al. (2016) Global analysis of seagrass restoration: the importance of large-scale planting. Journal of Applied Ecology 53:567–578. https://doi.org/10.1111/1365-2664.12562

van Tussenbroek B (2011) Dynamics of seagrasses and associated algae in coral reef lagoons. Hidrobiológica 21:293–310

Verduin JJ, Paling EI, van Keulen M, Rivers LE (2012) Recovery of donor meadows of *Posidonia sinuosa* and *Posidonia australis* contributes to sustainable seagrass transplantation. International Journal of Ecology 2012: 837317. https://doi.org/10.1155/2012/837317

Zhang Y-H, Li C, Zhao J-S, Li W-T, Zhang P-D (2021) Seagrass resilience: where and how to collect donor plants for ecological restoration of eelgrass *Zostera marina*. Ecological Engineering 158:106029. https://doi.org/10.1016/j.ecoleng.2020.106029

Zhou Y, Liu P, Liu B, Liu X, Zhang X, Wang F (2014) Restoration eelgrass (*Zostera marina* L.) habitats using a simple and effective transplanting technique. Plos One 9:e92982. https://doi.org/10.1371/journalpone0092982

Supporting Information

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

Figure S1. Particle size distribution of the sediments sampled on the donor meadow.

Coordinating Editor: Stephen Murphy

Received: 19 May, 2023; First decision: 20 September, 2023; Revised: 2 October, 2023; Accepted: 3 October, 2023