

Article

Patterns of Species Dominance in Two Coastal Restorations: Evidence of Sustained Seagrass Success over Long Time Scales

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Abstract

Restoration in coastal settings by reconstructing seagrass coverage after widespread loss has generally been monitored over a short time, with few studies extending ≥ 5 years. We assemble monitoring data available from two seagrass restoration areas in Florida, USA, to examine community development of benthic macrophytes from 1989 to 2025 after planting of the early successional seagrass, *Halodule wrightii*. Using field data collected at varying intervals, we (1) examined patterns of species persistence, investigating species replacement or persistence of benthic macrophyte taxa and (2) compared temporal patterns of species dominance in restored versus nearby natural reference sites. The pattern and tempo of seagrass expansion by *H. wrightii* at each of the two restoration areas differed. At Lassing Park, episodes of *H. wrightii* dominance were intermixed with a period of multi-species composition and co-dominance. After a bloom of the macroalga, *Caulerpa prolifera*, displaced seagrass in 2006, *H. wrightii* quickly recolonized the restoration site. At Shell Key, *H. wrightii* was the only species recorded at the restoration site over two decades. Species dominance by *H. wrightii* was recorded in both restoration and natural sites. Our findings illustrate the value of long-term monitoring for evaluating the resilience of restoration efforts and adopting extended monitoring programs. Such efforts would be enhanced by the genesis of innovative ideas for data collection and new methods for following the post-planting of seagrass.



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Keywords: seagrass; macroalgae; restoration; persistence; Florida; *Caulerpa prolifera*; *Halodule wrightii*

1. Introduction

Seagrass meadows, formed by marine angiosperms in subtidal waters rimming coastlines worldwide, have been increasingly recognized for their ecological and economic value [1]. The most extensive cover of seagrass in the USA is found along the Florida coast, where approximately 890,000 hectares of seagrass are composed of species with tropical-subtropical distributions [2]. The coastal waters of heavily populated Florida are strongly influenced by human interactions and, in some areas, past (e.g., Tampa Bay, 1950s [3]) and recent (e.g., Indian River Lagoon, 2019 to present [4]) seagrass loss has been recorded. Similar to other coastal wetland vegetation (mangroves and salt marshes) [5–8], restoration efforts utilizing planting of targeted seagrass species into sediments have been attempted in selected locales to reconstruct lost coverage of these valuable foundational species and to shorten their successional recovery after widespread meadow loss. Unlike other wetlands, the success of rebuilding underwater assemblages is highly influenced

by water quality and physical and biological disturbances that threaten the persistence of planted seagrass [9–11].

Recently, Rezek et al. [12] examined restoration studies conducted in Florida, largely available only in agency documents, that focused on rebuilding seagrass communities in shallow subtidal areas and noted that 88% of restoration sites, when revisited, supported seagrass, which greatly exceeds a reported global average (22–42%) [13]. Historically, evaluation of seagrass restoration success has been directed mainly at studies on temperate seagrass species (e.g., *Zostera marina*, *Posidonia oceanica*) [14–16]. However, in subtropical/tropical settings, the seagrass *Halodule wrightii* has been the overwhelmingly key species planted in restoration projects (e.g., [17,18]). Therefore, past reports on seagrass plantings and restoration success in subtropical/tropical settings have typically addressed the fate of this focal seagrass taxon, well known to be an opportunistic species [19].

In general, monitoring of seagrass restoration efforts has often been limited to a relatively short duration (1–3 years). Proportionately fewer studies have assessed restoration outcomes by continuing to monitor a site for ≥ 5 years post-planting [20–23]. In tropical/subtropical projects, longer-term monitoring can be especially critical, given that cover expansion by *H. wrightii* by this species occurs mainly by rhizome elongation [17], which can sometimes be slow. Moreover, after a disturbance, a diverse set of seagrass species may only develop after decades and subsequently reach full coverage of climax species in subtropical/tropical regions in Florida [24].

In this study, we assemble monitoring data available from two Florida restoration sites to examine patterns of seagrass community diversity over decades in restoration efforts initiated by the planting of *H. wrightii*, potentially providing a unique view of restoration outcomes in the subtropical setting. We focus on seagrass taxa but also include benthic macroalgae, as they have been historically present intermixed with seagrass in our region of interest. We thereby combine seagrass and macroalgae into a functional group of benthic macrophytes. Building upon earlier reports [21,25,26], we (1) examine patterns of species dominance, investigating potential species replacement or persistence of benthic macrophytes over this long time scale, and (2) compare patterns of species dominance in restored versus nearby natural reference sites to evaluate whether restored and natural assemblages display similar trajectories over the time period.

2. Materials and Methods

2.1. Restoration at Study Sites

Two seagrass restoration locations—Lassing Park (N 27.754612; W 82.628747) and Shell Key (N 27.668893, W 82.734690)—from the West Central Florida, USA coast (Figure S1) were chosen for study, given the unique decades of data available. The seagrass restoration effort at Lassing Park initiated in 1987 followed the filling of an expansive pre-existing swimming hole with dredged material and the subsequent planting of seagrass, *H. wrightii* [25,27]. Restoration of seagrass at Shell Key was initiated in 2002, also using planting units of *H. wrightii*. Median sediment grain size at both locations was 0.250 mm. Planting units of *H. wrightii* for both restoration locations were sourced from local nearby meadows. Specifics of planting design and methodology are available in [26]. Data collected on benthic macrophytes at these two restoration sites and companion natural seagrass beds were examined in this study.

2.2. Site Monitoring

Information on seagrass species identity and abundance of benthic macrophytes was gathered from a variety of published and unpublished studies/collections, including short-term surveys and long-term monitoring and experimental studies (Table 1) [28,29]. Data

collected was based on availability from both restoration and natural reference sites in the two locations. The frequency and mode of data collection varied over the decadal time scales, reflecting variation in funding sources and the nature of inquiry. Data were not available for all years at either location, although data were available from restored and natural sites for each year included in the investigation. Specific details of data collection at each of the restoration locations are presented below.

Table 1. Chronological listing of specific features of long-term data collection for benthic macrophytes at restoration and natural reference sites at Lassing Park (LP) and Shell Key (SK) locations. For each year for which data were available, information on sampling method and metrics is presented, along with the number of samples for each year. Data sources are from published and unpublished sources [12,21,25,26,28–30]. AGB = aboveground biomass; BB quadrats = macrophyte abundance from surveys. (V) = underwater video; (number in parentheses indicates the number of plots within which points were examined). See Figure S2 for more information on survey methods. * = unpublished data set, S. S. Bell.

Year	Survey Type	Number of Replicates	Data Source
(A) LP Restoration			
1989–1990	AGB cores	24	[25]
1991, 1993, 1994, 1998	AGB cores	12	*
2000–2001	AGB cores	12	[28]
2002–2007	AGB cores	10	*
2008	BB quadrats (v)	10	*
2010	AGB cores	10	*
2018	BB quadrats	30	[12]
2025	BB quadrats	5	[29]
(B) LP Natural			
1989–1990	AGB cores	24	[25]
1991, 1993, 1994, 1998	AGB cores	12	*
2000–2001	AGB cores	12	[28]
2002–2007	AGB cores	10	*
2008	BB quadrats (v)	10	*
2010	AGB cores	10	*
2018	BB quadrats	20	[12]
2025	BB quadrats	5	[29]
(C) SK Restoration			
2002–2005	BB points (12)	6000	[26]
2006	BB points (3)	1500	[21]
2007–2009	BB points (12)	6000	[21]
2018	BB quadrats	30	[12]
2024–2025	BB quadrats	5	[29]
(D) SK Natural			
2003	BB quadrats	18	[31]
2005	BB quadrats	10	[31]
2007	BB quadrats	15	[31]
2009	BB quadrats	16	[31]
2011	BB quadrats	16	[31]
2013	BB quadrats	11	[31]
2015	BB quadrats	9	[31]
2017	BB quadrats	8	[31]
2019	BB quadrats	11	[31]
2021	BB quadrats	14	[31]
2023	BB quadrats	15	[31]
2024–2025	BB quadrats	5	[29]

2.2.1. Lassing Park

At Lassing Park, two types of data reflecting species abundance were collected—aboveground biomass and Braun–Blanquet coverage abundance (BB score) of individual species of benthic macrophyte at both the restoration and natural reference sites. The natural reference site was 150–400 m away from the restoration site. Data were collected at varying intervals between 1989 and 2025. Aboveground biomass was assessed from 1989 through 2010 by taking cores at a frequency of 2–4 times per year. Given the nature of the available data, we assembled information on the percent composition of the aboveground biomass of

individual species of benthic macrophytes. The seasonal timing of the collection of cores and the total area sampled by cores varied across dates (Table 1). For each species, the percent composition by weight of the total biomass of benthic macrophytes was calculated for each year. Additionally, in 2008, 2018, and 2025, species contribution to the percent of benthic coverage was collected using visual surveys in the field or from underwater video. Coverage abundance was determined using the BB abundance (BB score) ranking method (i.e., [12,31]). Specifically, the percent cover of macrophytes was determined for each quadrat, and the cover score was converted to a BB rank. A mean BB score by year for each macrophyte taxon was calculated. This methodology for data collection was identical in natural and restoration sites.

2.2.2. Shell Key

All data on macrophyte abundance at Shell Key collected from field surveys were recorded using BB scores. The number of plots surveyed varied by date/year for each of the 12 planted plots. In each plot, 1500 points were ranked using BB scores to determine coverage abundance for the site. Each of the 12 plots was surveyed yearly through 2009, with the exception of 2006, when only 3 plots were surveyed [21,26]. Shell Key was reassessed in 2018, 2024, and 2025 using 5–30 haphazardly placed 0.25 m² quadrats within the restoration plots, and BB scores obtained on these dates. A natural seagrass bed adjacent to the restoration site, which is assessed annually using 0.25 m² quadrats as part of transect surveys in the Tampa Bay [30], was used as the natural reference site for cover abundance of benthic macrophytes in Shell Key.

2.3. Data Analysis

Dominance Index and Species Abundance

Seagrass meadows in Florida can be mono- or multi-specific, so the development of species abundance/diversity was of major interest after restoration planting of *H. wrightii*. We examined two metrics of community diversity: species abundance (number and identity of macrophytes) and dominance of benthic macrophytes for each restoration and reference natural site. Benthic diversity, as a count of the number of different species of benthic macrophytes present, was determined for natural and restoration sites at both Lassing Park and Shell Key locations. The dominance index [32] was calculated using data on aboveground biomass using the following:

$$DI = \frac{S}{T}$$

where **S** refers to the percent composition of a given species, and **T** represents the total percent composition (100%) of all species for each year. When datasets comprised surveys taken using BB scores, midpoint values for each BB category were used to assign a corresponding percent cover (BB) score (=TxEl values; addressed in [33]) for each species and year. For each year, mean TxEl values for an individual species were used as **S**, and the sum of TxEl for all species present was used as **T**. For our purposes, we consider species with a DI score ≥ 0.10 as a dominant species.

3. Results

3.1. Benthic Macrophyte: Identity and Abundance

3.1.1. Lassing Park

Halodule wrightii, the species selected for planting in 1987, was present in the Lassing Park restoration site for up to 17 years. Here, over time, the assemblage that emerged was composed of 1–4 benthic macrophytes, with *H. wrightii* being the taxon encountered most

consistently across all dates (Figure 1A,B). The greatest number of species present in the restoration site was recorded during 2010–2018, with *H. wrightii* being the only species encountered from 1990 to 1998 (Figure 1A). *Ruppia maritima* was found infrequently at the restoration site but was absent from natural sites (Figure 1A,D). Likewise, *Syringodium filiforme*, an uncommon taxon encountered at the restoration site, contributed to a large proportion of seagrass cover at natural sites in 2018. In 2025, *H. wrightii* was essentially a monospecific assemblage across restoration and natural sites.

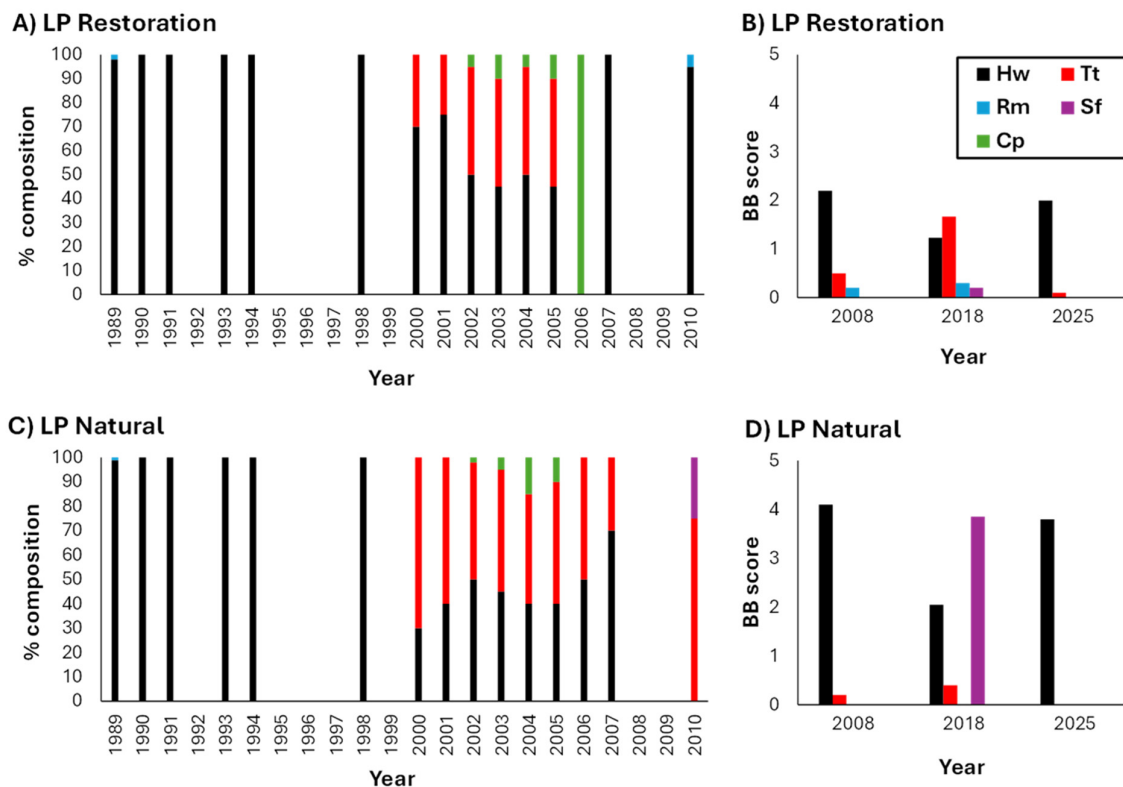


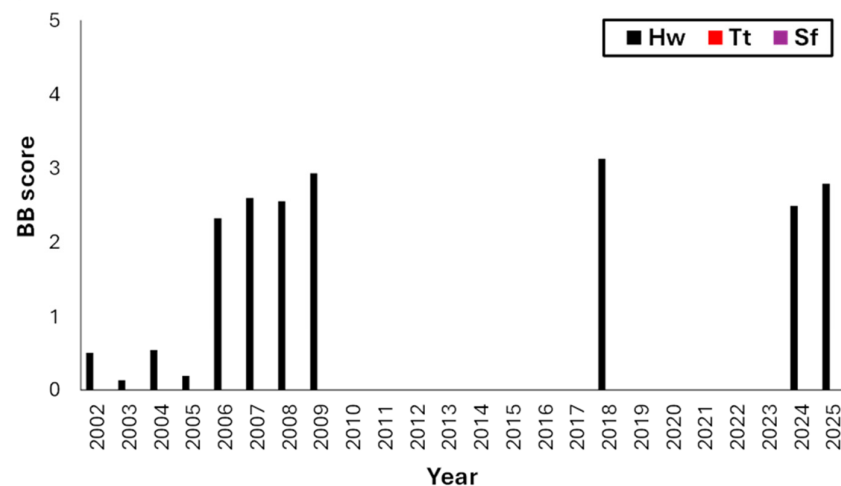
Figure 1. Abundance of benthic macrophyte taxa at Lassing Park (LP), Florida, USA. Percent composition of benthic macrophyte taxa from 1989 to 2010 (A,C) and mean BB score of benthic macrophyte taxa from 2008, 2018, 2025 (B,D) are shown for restoration (A,B) and natural (C,D) sites. Benthic macrophyte taxa: *Halodule wrightii* (Hw), *Thalassia testudinum* (Tt), *Ruppia maritima* (Rm), *Syringodium filiforme* (Sf), and *Caulerpa prolifera* (Cp). See Table 1 for details about sampling efforts for each year.

In restoration and natural sites at Lassing Park, *H. wrightii* and *T. testudinum* together composed the largest percentage of benthic macrophyte biomass in samples over 18 years after initial seagrass plantings (Figure 1A,D). However, only *Caulerpa prolifera* was found in restoration plots in 2006. After being completely absent in 2006, *H. wrightii* was again recorded in 2007 at the restoration site and in all subsequent sampling dates as either a monospecific or in a mixed assemblage accompanied by 1–3 other seagrass taxa. Although *C. prolifera* was also present in the natural sites at Lassing Park prior to 2006, it never attained comparably high levels of cover similar to that recorded in the restoration site. Instead, both *H. wrightii* and *T. testudinum* maintained relatively similar patterns of species presence after the initial 11 years and together composed the majority of seagrass biomass across all years at the natural sites. In 2010, *T. testudinum* and *S. filiforme* were the only two species of seagrass recorded at the natural site.

3.1.2. Shell Key

At Shell Key, the seagrass *H. wrightii* was the lone species recorded at restoration sites across the 22 years post-planting (Figure 2A). Low cover of seagrass during the beginning phases of seagrass plot development (through 2005) was followed by a persistent level of moderate cover by *H. wrightii* through to the most current sampling date. In natural sites, *H. wrightii* consistently maintained moderate levels of benthic cover over all dates, with two additional seagrass species—*T. testudinum* and *S. filiforme*—displaying low levels of cover from 2010 to 2023 (Figure 2B). No benthic macroalgae were found at Shell Key.

A) SK Restoration



B) SK Natural

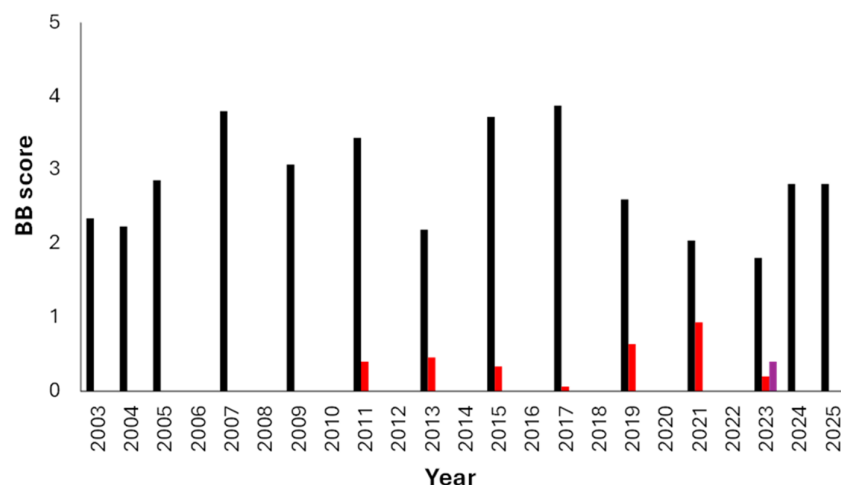


Figure 2. Abundance of benthic macrophyte taxa at Shell Key (SK), Florida, USA. Seagrass was planted in 2002. Mean BB score of benthic macrophyte taxa at restoration (A) and natural (B) sites from 2003 to 2025. Benthic Macrophyte taxa: *Halodule wrightii* (Hw), *Thalassia testudinum* (Tt), and *Syringodium filiforme* (Sf). See Table 1 for details about sampling efforts for each year.

3.2. Benthic Macrophyte Dominance

When viewed over all dates combined (Figure 3), *H. wrightii* displayed clear dominance by biomass or cover. Among the five species of benthic macrophytes recorded at natural and restoration sites at Lassing Park, *H. wrightii* had the highest dominance index in 16 out of 18 dates in restoration sites (Figure 3A) and in 10 out of 16 dates in natural sites (Figure 3B) (Table 2). The seagrass *T. testudinum* had the second highest dominance index at both reference and restoration sites over a similar period (Figure 3A,B). In Shell Key, the

mean dominance index for *H. wrightii* at both restored and natural sites over all dates again indicated dominance of spatial cover by *H. wrightii* with but negligible contribution by two other seagrass species (Figure 3C,D) (Table 2).

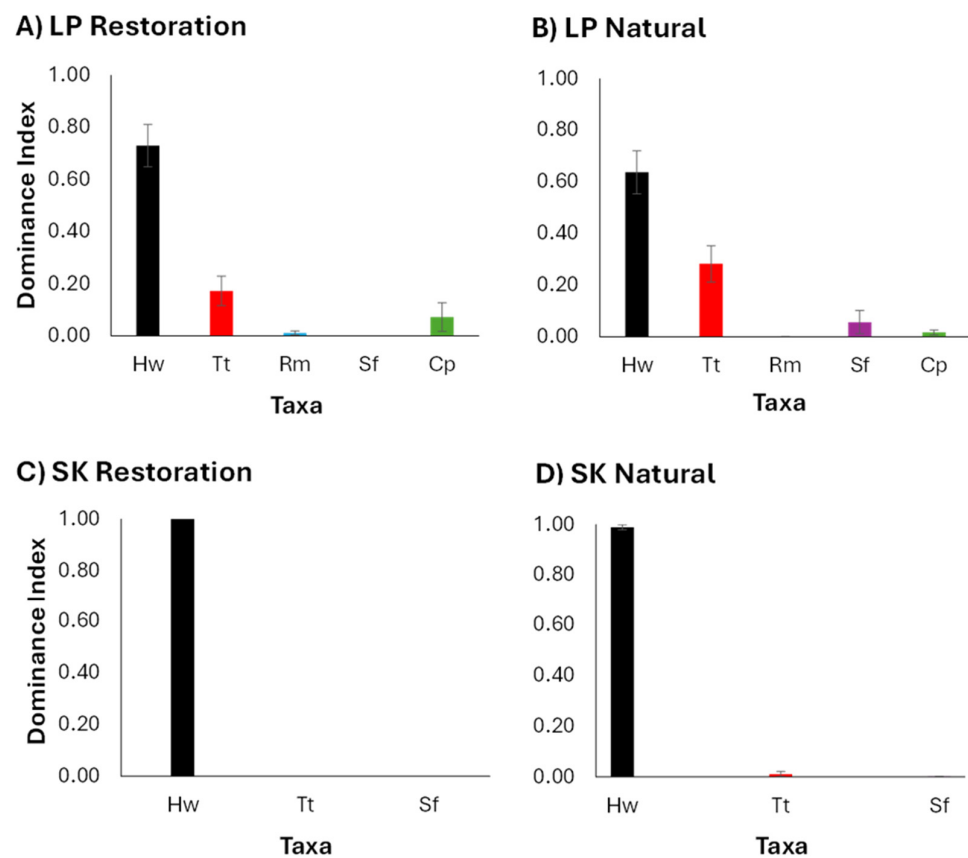


Figure 3. Dominance indices (DI) (mean $\pm$ SE) of benthic macrophyte species at Lassing Park restoration (A), Lassing Park natural (B), Shell Key restoration (C), and Shell Key natural (D) sites. Benthic macrophyte taxa: *Halodule wrightii* (Hw), *Thalassia testudinum* (Tt), *Syringodium filiforme* (Sf), *Ruppia maritima* (Rm), *Caulerpa prolifera* (Cp).

Table 2. Count of the number of years during which a benthic macrophyte taxon was dominant. Total sample years varied by site and location: for Lassing Park (LP), either Natural or Restoration sites, $n = 18$; for Shell Key (SK) Restoration, $n = 11$; for Shell Key (SK) Natural, $n = 14$.

	LP		SK	
	Restoration	Natural	Restoration	Natural
<i>Halodule wrightii</i>	16	17	11	14
<i>Thalassia testudinum</i>	7	9	0	1
<i>Syringodium filiforme</i>	0	2	0	0
<i>Caulerpa prolifera</i>	3	9	0	0

4. Discussion

Our investigation into the diversity of two restoration studies offers a collective view of the dynamics of benthic macrophyte assemblages in a subtropical marine setting. Our synthesis of data spanning almost two decades of monitoring of mainly seagrass communities revealed a compelling example of convergence of restored and natural sites at each of two areas (Shell Key and Lassing Park) based upon species dominance, macrophyte identity, and number of taxa. This unique data set provides evidence that *H. wrightii*, the

seagrass used as planting units in restoration at each location, displayed not only successful establishment but also persistence when viewed over this time period. Up to five species of benthic macrophytes were encountered in the data collection, but assessment of restoration response was focused on one taxon, *H. wrightii*, that overwhelmingly dominated measures of biomass or cover.

While similar patterns of community development, especially species dominance, were recorded between the two restoration sites, the pattern and tempo of seagrass expansion by *H. wrightii* at the restoration sites differed. At Lassing Park, the dominant seagrass, *H. wrightii*, demonstrated continuous colonization of bottom sediments after planting. Recovery of the seagrass taxon after the bloom of the benthic macroalga, *C. prolifera* in 2006 was evident in 2007. In contrast, at Shell Key, an initially slow rate of expansion of seagrass coverage was followed by a substantial increase in *H. wrightii* coverage during 2006 [21]. Comparison of restoration dynamics between Lassing Park and Shell Key areas from 2010 to 2023 is somewhat limited by a reduced data set, and some dynamic changes in benthic macrophytic species may have been undetected. Yet, despite some differences in community development between areas in 2018 and 2024 during which three major hurricanes passed over both Lassing Park and Shell Key, similar patterns of *H. wrightii* dominance have continued.

In addition to dominance by *H. wrightii* in restoration sites at Lassing Park, other benthic macrophyte species periodically contributed greater than 10% ($DI \geq 0.10$) to total macrophyte abundance, consistent with our definition of dominance (Figure 3). Most notable was *C. prolifera*, which represented only a low to moderate proportion of macrophyte abundance in 2002–2005 in both restoration and natural sites at Lassing Park. However, *C. prolifera*, increasing to 100% of macrophyte abundance in 2006 at the restoration site at Lassing Park, was notable. Stafford and Bell [34] found that *C. prolifera* can out-compete *H. wrightii* for space, and this may explain, in part, the rapid increase in the benthic macroalga. *Halodule wrightii* recovery after the macroalgal bloom ended may have been expedited by colonization by fragments transported to the area [35]. Additionally, recovery in the restoration area could have been the result of colonization from local seagrass beds or from remnant shoots/rhizomes of *H. wrightii* that remained after *C. prolifera* declined. Interestingly, *C. prolifera* has not reappeared at Lassing Park restoration or natural sites since 2006. Such algal boom and bust characteristics and coordinated loss of seagrass have been noted in other systems (e.g., Canary Islands [36]) but, overall, remain poorly explained.

The dominance of *H. wrightii* at restoration sites reflects patterns seen in natural seagrass beds throughout shallow subtidal waters in the Tampa Bay [37], following trends widely reported in other areas such as the east coast of Florida [38], south Florida [39], and coastal waters of Texas [40,41]. The life history characteristic of *H. wrightii* as comparatively fast-growing [19] underlies the selection of *H. wrightii* as a popular primary source of planting units in restoration studies, as rapid development of broad seagrass coverage is often a goal. Dominance of *H. wrightii* during early stages of community succession has been documented from deeper seagrass beds in Florida Bay, and this seagrass has been recognized as the taxon appearing at first/early stages of seagrass recovery following die-off [24]. *Halodule wrightii* dominance does not persist in deeper waters of Florida Bay, where it is typically replaced by later successional stage species—*S. filiforme* and *T. testudinum* [24]. We expect that *H. wrightii* will likely continue to be utilized for restoration in coastal regions like those rimming Tampa Bay, given its demonstrated persistence in restoration sites and its consistent presence in natural sites in coastal locations.

Our multidecadal examination of restoration outcomes provided an opportunity to evaluate a complex set of responses by the benthic macrophytic community. Rezek et al. [12] revisited restoration sites of varying ages in Florida and reported that 60% of studies older

than 5 years had the same or greater number of species in restoration sites compared to those at natural sites. This relationship appears to be true at Lassing Park and Shell Key after the first five years. Specifically, at Lassing Park, we did not see a trajectory of continual increase in the number of species or evidence of successional patterns of *H. wrightii* being replaced by *T. testudinum*/*S. filiforme* over time. Rather, episodes of *H. wrightii* dominance were intermixed with a period of multi-species composition and co-dominance (2006–2018). Displacement of *H. wrightii* by *Caulerpa* may have impacted the successional development of a multi-species community at Lassing Park. At Shell Key, *H. wrightii* was the only species recorded at the restoration site over two decades. In 2011–2023, *T. testudinum* and *S. filiforme* occurred at very low abundances (not meeting our criteria for dominance) in natural sites at Shell Key. In 2024 and 2025, *H. wrightii* dominance prevailed in both restoration and natural sites at Lassing Park and Shell Key, and no consistent pattern of additional species occupation persisted across time at any site.

Long-term monitoring of seagrass restoration, as shown here, offers an additional perspective on the persistence of restoration efforts and supports the efficacy of these management strategies. Clearly, some of the more intriguing patterns of response by seagrasses and a macrobenthic alga, such as the algal bloom and seagrass recovery at Lassing Park in 2007 and the delayed then rapid increase and sustained dominance of *H. wrightii* 2006–2025 at Shell Key, would have been undetected with short-term monitoring. Our findings support the conclusion that future monitoring using a combined approach that includes both short- and long-term assessments offers the opportunity for increased detection of species loss and recovery as part of a post-restoration history. Although the benefits of long-term monitoring are obvious and can potentially address calls for assessing the permanency of restoration projects, the logistics of assembling the needed information remain challenging unless some mechanism for direct funding of project assessment over decadal time periods exists. It is likely that developing partnerships with community groups, governmental agencies, and educational institutions might be the best option when funding is extremely limited or unlikely to be championed. Innovative ideas and new methods for following the post-planting of seagrass could expedite the adoption of extended monitoring programs. Communicating the value of long-term studies of restoration projects supported by demonstrated findings is an essential step in attracting support for such efforts.

Supplementary Materials: The following supporting information can be downloaded at <https://www.mdpi.com/article/10.3390/d17120832/s1>, Figure S1. Map displaying two study locations. Lassing Park (purple) and Shell Key (orange) and Restored (star) and Natural sites (circle). Figure S2. (A). Example of planted seagrass unit of *Halodule wrightii*. Sampling collection techniques used to follow seagrass bed development included use of (8–10 cm diameter) cores (B) to collect seagrass aboveground biomass, field visual surveys of benthic macrophyte presence in quadrats (C) emplaced in the field, and quadrats emplaced on digital images to quantify macrophyte presence from underwater video collected with a camera on a benthic sled (D) representing a 0.5 m × 1.0 m field of view.

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Abbreviations

The following abbreviations are used in this manuscript:

N North Latitude

W West Longitude

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