COMPARATIVE GROWTH AND DEMOGRAPHICS OF THALASSIA TESTUDINUM MEADOWS IN CUBA USING DIRECT AND RECONSTRUCTIVE METHODS APPROACHES TO INFORM CONSERVATION EFFORTS

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ABSTRACT

Efforts in establishing accurate and affordable methods for monitoring the status of seagrasses provide reliable information about growth and demographics that contribute to informed management decisions. Here we compared the use of reconstructive and direct census analyses to understand the dynamics of Thalassia testudinum. Both, the reconstructive and census methods, show a similar rate of leaf production and vertical growth rates, which is among the highest reported for Thalassia. Results also show that the calculation of mortality and recruitment differed between the reconstruction and census methods, with the latter showing a higher recruitment rate. Outcomes indicate that although reconstruction methods can provide reliable insight on seagrass dynamics, censuses provide more accurate demographics. Direct census methods are proposed as a more reliable approach to assess seagrass demographics after extreme weather events, while indirect methods show appropriate as a more economical alternative for long-term monitoring.

INTRODUCTION

Seagrasses are highly productive ecosystems, providing food, habitat, and shelter to a large number of micro- and macroorganisms, as well as an array of goods and services benefiting human development [1-4]. As ecosystem engineers, seagrasses modify their immediate physical environment attenuating the effect of water flow and stabilizing sediments by preventing or reducing their resuspension. As such, seagrasses contribute to improving water transparency and provide coastline protection [5, 6]. estimated that seagrass and algae beds offer services with a value of $28,916 ha−1 yr−1, accounting for climate regulation, erosion control, nutrient cycling, refuge, food production, raw materials, genetic resources, recreation, and cultural services. In Cuba, [7] recognized that seagrass meadows, along with coral reefs and mangroves ecosystems, are critical for the sustainability of fisheries. Moreover, using 2002 carbon emission data, [8] estimated that local meadows sequester 33% of the total carbon emitted by the country highlighting the importance of protecting the meadows. Cuban seagrass meadows have been drastically affected or have disappeared completely due to anthropogenic pressure including mechanical disturbance, fishing effort and terrestrial discharges or lack of run-off but also by climate-driven events such as storms and hurricanes [7]. As a result, there is an increasing effort in establishing accurate and affordable methods for monitoring their status that can provide reliable information about their growth and demographics. The goal is developing plans for the protection of seagrass meadows around Cuba while maintaining regional and sustainable development. The dominant seagrass species in Cuba, as in all the Caribbean Sea, is Thalassia testudinum [9, 10]. The paucity of species in the seagrass flora (i.e., 66 species sensu [11]) is reflected in the low species diversity in the communities they form, with about half of the meadows

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described in the literature being monospecific \[1\]. Seagrasses share a similar architecture formed the repetition of basic modules, which extend laterally to colonize available substrates \[12\][13\]. This similarity across species suggests that this modular architecture plays a key role in their adaptive capacity providing valuable elements to predict their ecological behavior \[14\]. The basic architectural modules consist of 1) rhizome internodes with which the plant ensures its horizontal or vertical vegetative extension, 2) leaves that responsible for photosynthesis and nutrient uptake from the water column, and 3) roots, which provide the anchoring system and contribute to nutrient absorption from the sediment \[15\][16\]. The rate at which clonal extension occurs can differ by up to a factor of 50 among species \[17\]. For example, some species like *Posidonia oceanica* exhibit a slow growth rate resulting in an extension of < 10 cm per year \[17\], while others like *Halophila ovalis* and *Syringodium filiforme* can extend more than 5 m per year \[12\]. Seagrasses maintain continuous clonal growth (i.e., recruitment) to compensate for mortality while occupying available substrates \[14\][13\]. As such, the dynamics of seagrass meadows are often linked to the dynamics of their substrate. Erosion, for example, generates mortality of the meadows by exposing rhizomes and roots, thus increasing the probability for detachment, and opening spaces for other benthic competitors \[15\][1\]. Sediment burial also generates mortality by blocking or reducing the availability of light \[13\][3\]. However, sediment accumulation could later facilitate seagrass colonization by increasing the availability of substrate. Although there is great interest in the conservation of seagrasses in Cuba, to date, there is no extensive assessment of the state of its meadows. There are, however, few studies describing direct censuses done to evaluate seagrass from the North Coast of Cuba \[18\][19][16][20][21\]. Although effective in assessing the status and population dynamics of *Thalassia testudinum*, direct censuses are laborious and rarely selected as the approach to create long time-series data in Cuba. Despite the lack of direct censuses in which growth is measured by marking leaves, rhizomes or shoots, development in seagrasses can also be addressed by reconstructing past growth from plant anatomical patterns \[22\]. For example, the plastochron interval (i.e., time interval between two successive anatomical events, such as leaf formation, sensu \[23\]) can be used as a reconstructive method to determining the growth of seagrass by measuring the expansion of vegetative tissue on individual shoots over time, taking into account the various seagrass morphological growth forms \[22\]. This method was first used to measure foliar production of *Zostera* \[24\] and later, foliar and rhizome production in *Thalassia testudinum* \[25\].

Since then, reconstructive methods have been used to determine different aspects of the ecology of seagrasses such as estimation of periodic changes in the length of rhizome intervals; age differentiation of shoot cohorts, and consecutive flowering events \[26-32\]. The present investigation reports on a comparative analysis of growth and demographics of *Thalassia testudinum* meadows in Sabana-Camagüey Archipelago, Cuba, using direct and reconstructive methods. We also report on the effectiveness of using both methods and an assessment of sediment dynamics as complementary to evaluate the effect of sediment dynamics on the status of seagrass meadows.

### MATERIALS AND METHODS

#### Study Site

The study was conducted in the Northern keys of Ciego de Avila province in the Sabana-Camagüey Archipelago, on the NW platform of Cuba (Figure 1). Seagrass meadows along the Sabana-Camagüey Archipelago are formed mainly by *T. testudinum* and occasionally mixed with *Halodule wrightii* and *Syringodium filiforme* \[33\][10\]. Cayo Coco- Cayo Romano region exhibits intense coastal dynamic regimes modulated by waves and wind and directly influenced by hurricanes and cold fronts \[34\]. The beach at site shows a general trend to erosion. The average salinity is 36.7 ppm and the transparency of the water usually exceeds 18 m \[35\].

Five sampling stations, were selected based on the maximum depth of seagrass meadows and the relationship between sediment granulometry and dynamics with meteorological event. The average depth within each station ranged from 0.75 m to 3.5 m. The total extension of the meadows per sampling station was obtained by deploying transects parallel and perpendicular to the coast, ensuring to include the upper- and lower-most limits per meadow. Coastal dynamics data were taken from CIEC Coastal Dynamics group database, which performs monthly measurements at the sampling stations using a LEICA T460 electronic theodolite. For each measurement, slope variations, as well as diameter of sand particles, were collected to determine distance and unevenness values at given points. These measurements were used to calculate volumes of sediment transport across the meadows and to construct beach profiles of a given distance and depth per sampling station.

#### Demography and population structure

Approximately 92 ± 3 shoots per sampling station were cleared of their leaf sheaths to expose the nodules in the vertical rhizomes completely. All vertical nodules and leaves per shoot were counted and converted to proxies of chronological age by multiplying the number of internodes and green leaves per shoot by their PI (see below) calculated using reconstruction or census methods \[22\]. Foliar biomass for the five sampling stations was estimated following the protocols described in \[10\], in which all the foliar biomass collected with the cores was dried to obtain constant dry weight. Leaves collected were separated from the shoots, cleaned from epiphytes, decalcified, and dried at 60 °C until constant weight. The density of shoots for Larga, Petrolera and Flamingo stations was estimated directly using the number of shoots marked per quadrat for the census. In Antón and Paredón, density was estimated by quantifying the total number of shoots within three 50 cm quadrats placed randomly along a 100 m transect.

Mortality, recruitment, and net population growth were calculated using both indirect and direct methods. For all sampling stations, reconstruction method estimates of specific mortality \(M_{ESP\text{-year}^{-1}}\), recruitment \(R_{ESP\text{-year}^{-1}}\), and net population growth \(CNP_{ESP\text{-year}^{-1}}\) were determined using the statistical mode of age estimates previously calculated. The following were used:

\[
M_{ESP} = \frac{(N_t/N_0)}{t}
\]

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**References**

R ESP = \frac{\ln (N \text{tot}/Nt)}{t}

CNP ESP = R ESP - M ESP

Where \(N_t\) is the number of shoots older than the statistical mode, \(N_0\) is the number of shoots with the same age as the statistical mode, \(N_{\text{TOT}}\) is the number of total shoots and \(t\) is the age of the shoots in the statistical mode (one year old in this case).

Direct census estimates were conducted for 12 consecutive months only for Larga, Petrolera, and Flamingo stations. On average, 178 ±7 shoots per quadrat per station were marked using the puncturing technique described, with a total of approximately 1601 shoots marked across stations. Quadrats were visited every four months, and surviving shoots were quantified, while new ones were quantified and marked using a different puncture pattern. In addition to specific estimates, this method also allowed calculating yearly absolute mortality (M, shoots m\(^{-2}\) d\(^{-1}\)), recruitment (R, shoots m\(^{-2}\) d\(^{-1}\)) and net population growth (CNP (shoots m\(^{-2}\)year\(^{-1}\))). The following equations were used:

\[ M = \frac{(N_0 - S)}{At} \]
\[ R = \frac{N_1 - S}{At} \]
\[ M \text{ ESP} = \frac{\ln (N_0)}{t} \]
\[ R \text{ ESP} = \frac{\ln (N_t)}{t} \]
\[ CNP \text{ ESP} = \frac{(Nt - NO)}{At} = R - M \]

CNP ESP = R ESP - M ESP

Where \(N_0\) is the number of shoots marked at the beginning of each observational period, \(N_1\) the number of shoots present at the end of each observation period, \(S\) is the number of shoots that survived, \(A\) is the total area per quadrat (m\(^2\)), and \(t\) is the day interval between observations.

**Determination of the plastochron interval (PI)**

**Reconstruction method:** Approximately 100 samples per station were collected using PVC cores of 15 cm in diameter and 70 cm in height. Samples consisted of 50 cm deep sediment cores that were washed carefully to collect individual seagrass modules of *T. testudinum*, ensuring that the connection between the horizontal and vertical rhizomes remained intact. These basic modules, including leaves and rhizomes, were used to determine the plastochron interval (PI) indirectly, which then allowed estimating the vertical growth rate and age of offspring.

Once cleaned, five of the most mature modules per sampling station were selected and the length of each internode from the apex to the oldest section of each module was measured. The variability of length across internodes was then filtered using a long-pass filter to eliminate the annual variability and a short-pass filter to extract the seasonal signal of plant growth. Data filtering further allowed to assess the number of internodes produced in one year (i.e., a cycle) as described in\[^{27}\]\[^{22}\]. The average PI was determined from the average estimates of the number of leaves produced in each of the identified cycles.

**Census method:** Three 10 x 20 cm quadrats per sampling station were marked in Flamingo, Petrolera, and Larga stations to obtain a direct measurement of the PI. All shoots within the quadrats were punctured immediately above the foliar sheath\[^{36}\] and collected 10 to 11 days later. This process was repeated four times within 12 months. The PI was then calculated as:

\[ \text{PI} = \frac{\text{number of shoots marked} \cdot \text{days}}{\text{number of new leaves with no marks}} \]

Where the number of days corresponds to either 10 or 11 based on interval between puncturing and collection of shoots.

**Analysis**

The average and standard error were calculated for each variable, except for age estimates for which the median was determined as the best indicator of the central tendency of the data. The Student t-test was used to determine if there were differences in the PI calculated by the reconstruction or census methods. The relationship between the variables of coastal dynamic and seagrass biomass per meadow was determined by linear regression of least squares between the two. All analyses were performed with STATISTICA v. 7.\[^{37}\] and Beach Profile Analysis Toolbox v. 3.2\[^{38}\].

Studies on the allometric relationship between shoot biomass and their spacing indicate that the basic clonal architecture of the species reflects the state of development of a meadow, with shoot density and biomass showing a close correlation. In this study, we calculated the upper limits of biomass and density of *T. testudinum* that each sampling station could reach.

**RESULTS**

The average extension of the meadows was 2045 ±1047 m, with Larga station showing the smallest extension (i.e., 250 m) and Antón the largest (i.e., 5000 m). Antón sampling station also showed the deepest limit, with a maximum depth of 11 m (Table 1).

The average shoot density across stations was 771.9 ± 48.9 shoots m\(^{-2}\), with density varying between 668 ± 93 shoots m\(^{-2}\) in Larga and 925 ± 138.4 shoots m\(^{-2}\) in Flamingo. Foliar biomass was calculated at an average of 165.9 ± 12.0 g m\(^{-2}\), with Petrolera station showing the lowest value (i.e., 135.1 ± 9 g m\(^{-2}\)) and Paredón the highest (i.e., 191.3 ± 24.5 g m\(^{-2}\)) (Table 2).

The PI determined using the reconstruction method was calculated as 10.8 ± 0.7 days. The reconstruction method showed that leaf production follows a clear annual cycle with two peak periods (Figure 2). The average number of internodes produced in a cycle, which is equal to the average number of leaves produced per year, was 34 ± 2. On the other hand, the census indicated a PI of 11.8 ± 0.31 days, equivalent to forming 31.2 ± 0.8 leaves per year. No statistical difference (Student t > 0.05) were detected in the PI calculated by either method. As such, estimates derived from the census method were used to transform estimates of in PI units to chronological time (i.e., days or years).
The half-life of the shoots collected varied across the five sampling stations, with shoots from Larga showing the lowest mean expand (i.e., 347 days) but also the oldest shoot (i.e., 1755 days), while Paredón showed the longest mean expand (i.e., 470 days) (Table 2).

The estimates of mortality obtained with the reconstructive method indicated a higher rate of mortality than recruitment for all stations except at Larga (Table 3). Contrarily, the census showed that recruitment, both absolute and specific, was higher than the mortality at all stations (Table 4). Shoots recruited at an average of 163 ± 10 shoots m⁻² during the 12-month sampling period, with Flamingo showing the lowest average (i.e., 131 ±13) and Larga the highest (184 ± 12). Overall survival rates across sampling stations was high (Fig 3), with Petrolera showing the lowest (i.e., 89. 9 %) and Larga the highest (92.2 %).

The granulometric features of the sediments collected across all sampling stations indicate moderate hydrodynamic regimes with low slope profiles according to the Wentworth classification [14]. All stations showed a sandy substrate with size grains of av. 0.28 ± 0.006 mm in diameter. From all stations, Paredón showed the greatest change in sand volume, while Larga the least at the same period.

For all stations, there was a foliar biomass difference as a function of sediment dynamics (Fig 4).

**Figure 1** Study sites in Sabana-Camagüey Archipelago (•, sampling stations). (Flamingo [22°32'39.7"N; 78°25'48.2"W], Larga [22°32'18.2"N; 78°21'42.6"W], Petrolera [22°32'41.3"N; 78°35'34.0"W], Paredon[22°27'08.4"N; 78°07'52.0"W] and Antón [22°24'48.0"N; 78°04'50.5"W]).

**Figure 2** Sequence in the length of internodes for one seagrass shoot of T. testudinum collected from Flamingo station. Arrows indicate the maximum peaks within a cycle.

**Figure 3** Average recruitment, ±SE and survival (%) of T. testudinum shoots from Larga (A), Flamingo (B) and Petrolera (C) stations in Sabana-Camaguey, NW Cuba between between 2018-2019.

**Figure 4** Correlation (r² = 0.81, p < 0.005) between foliar biomass per station and difference in volume of sand along profiles across five meadows of T. testudinum in Sabana-Camaguey Archipelago, NW Cuba between between seagrass biomass and differences in sand volume.

**Figure 5** Relationship between shoot density and biomass in each sampling station. The line indicates the theoretical maximum biomass and density that could be reach.
Table 1 Extension of seagrass meadows and average shoot density and foliar biomass of seagrasses across five sampling stations in Sabana-Camaguay archipelago, NW Cuba.

<table>
<thead>
<tr>
<th>Factors</th>
<th>Flamingo</th>
<th>Larga</th>
<th>Petrolera</th>
<th>Paredón</th>
<th>Antón</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lower limit (m)</td>
<td>5.0</td>
<td>8.2</td>
<td>9.3</td>
<td>10.0</td>
<td>11.0</td>
</tr>
<tr>
<td>Upper limit (m)</td>
<td>0.6</td>
<td>2.5</td>
<td>0.75</td>
<td>1.4</td>
<td>1.2</td>
</tr>
<tr>
<td>Biomass (g m⁻²)</td>
<td>±3.15</td>
<td>±29.4</td>
<td>±9.0</td>
<td>±24.5</td>
<td>±19.5</td>
</tr>
<tr>
<td>Shoot density</td>
<td>±93.7</td>
<td>±53.5</td>
<td>±13.1</td>
<td>±63.5</td>
<td>±138.4</td>
</tr>
</tbody>
</table>

Table 2 Half-life expand (± SE), maximum age, and vertical growth rate (± SE) of T. testudinum collected from Antón, Larga, Flamingo, Paredón, and Petrolera stations in Sabana-Camaguay, NW Cuba.

<table>
<thead>
<tr>
<th>Factors</th>
<th>Flamingo</th>
<th>Larga</th>
<th>Petrolera</th>
<th>Paredón</th>
<th>Antón</th>
</tr>
</thead>
<tbody>
<tr>
<td>Half-life expand (days) ±SE</td>
<td>370.8 ±33.0</td>
<td>347.2 ±35.7</td>
<td>364.9 ±26.2</td>
<td>470.8 ±27.1</td>
<td>388.4 ±22.3</td>
</tr>
<tr>
<td>Age (days)</td>
<td>1684.8</td>
<td>1755.0</td>
<td>347.2</td>
<td>1035.0</td>
<td>936.0</td>
</tr>
<tr>
<td>Vertical growth (mm PI)</td>
<td>5.6 ±0.5</td>
<td>6.1 ±0.3</td>
<td>745.3 ±6.6</td>
<td>800.0 ±6.6</td>
<td>925.0 ±3.7</td>
</tr>
</tbody>
</table>

Table 3 Specific mortality, specific recruitment, and net population growth of seagrass meadows of T. testudinum from Antón, Larga, Flamingo, Paredón, and Petrolera stations in Sabana-Camaguay, NW Cuba obtained using reconstructive methods directs.

<table>
<thead>
<tr>
<th>Factors</th>
<th>Flamingo</th>
<th>Larga</th>
<th>Petrolera</th>
<th>Paredón</th>
<th>Antón</th>
</tr>
</thead>
<tbody>
<tr>
<td>M² (year⁻¹)</td>
<td>0.25</td>
<td>0.75</td>
<td>1.05</td>
<td>0.51</td>
<td>1.58</td>
</tr>
<tr>
<td>R² (year⁻¹)</td>
<td>0.69</td>
<td>0.85</td>
<td>0.79</td>
<td>0.41</td>
<td>0.62</td>
</tr>
<tr>
<td>CNP (year⁻¹)</td>
<td>-0.04</td>
<td>0.09</td>
<td>-0.24</td>
<td>-0.10</td>
<td>-0.96</td>
</tr>
</tbody>
</table>

Table 4 Demographics of seagrass meadows of T. testudinum from Larga, Petrolera, and Flamingo stations in Sabana-Camaguay, NW Cuba during the sampling periods using a census approach. M (absolute mortality), R (absolute recruitment), CNP (absolute net population growth), M² (specific mortality), R² (specific recruitment), and CNP² (net population growth).

<table>
<thead>
<tr>
<th>Months</th>
<th>Larga</th>
<th>Petrolera</th>
<th>Flamingo</th>
<th>M ±SE</th>
<th>R ±SE</th>
<th>M² ±SE</th>
<th>R² ±SE</th>
<th>CNP ±SE</th>
<th>M² (year⁻¹)</th>
<th>R² (year⁻¹)</th>
<th>CNP² (year⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Jul</td>
<td>0.15±</td>
<td>0.22±</td>
<td>0.17±</td>
<td>0.05±</td>
<td>0.01±</td>
<td>0.00±</td>
<td>0.00±</td>
<td>0.00±</td>
<td>0.30±</td>
<td>0.17±</td>
<td>0.00±</td>
</tr>
<tr>
<td>Aug</td>
<td>0.00±</td>
<td>0.02±</td>
<td>0.02±</td>
<td>0.00±</td>
<td>0.00±</td>
<td>0.00±</td>
<td>0.00±</td>
<td>0.00±</td>
<td>0.30±</td>
<td>0.17±</td>
<td>0.00±</td>
</tr>
<tr>
<td>Sep</td>
<td>0.13±</td>
<td>0.06±</td>
<td>0.11±</td>
<td>0.03±</td>
<td>0.00±</td>
<td>0.00±</td>
<td>0.00±</td>
<td>0.00±</td>
<td>0.30±</td>
<td>0.17±</td>
<td>0.00±</td>
</tr>
<tr>
<td>Oct</td>
<td>0.07±</td>
<td>0.08±</td>
<td>0.01±</td>
<td>0.00±</td>
<td>0.00±</td>
<td>0.00±</td>
<td>0.00±</td>
<td>0.00±</td>
<td>0.30±</td>
<td>0.17±</td>
<td>0.00±</td>
</tr>
<tr>
<td>Nov</td>
<td>0.16±</td>
<td>0.16±</td>
<td>0.13±</td>
<td>0.04±</td>
<td>0.00±</td>
<td>0.00±</td>
<td>0.00±</td>
<td>0.00±</td>
<td>0.30±</td>
<td>0.17±</td>
<td>0.00±</td>
</tr>
<tr>
<td>Dec</td>
<td>0.19±</td>
<td>0.21±</td>
<td>0.20±</td>
<td>0.05±</td>
<td>0.00±</td>
<td>0.00±</td>
<td>0.00±</td>
<td>0.00±</td>
<td>0.30±</td>
<td>0.17±</td>
<td>0.00±</td>
</tr>
</tbody>
</table>

Table 5 Average sand diameter and differences in sand volume in meadows of T. testudinum in Sabana-Camaguay Archipelago, NW Cuba between March and September.

<table>
<thead>
<tr>
<th>Factors</th>
<th>Larga</th>
<th>Petrolera</th>
<th>Flamingo</th>
<th>Paredón</th>
<th>Antón</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sand diameter (mm)</td>
<td>0.27</td>
<td>0.29</td>
<td>0.26</td>
<td>0.28</td>
<td>0.27</td>
</tr>
<tr>
<td>Difference sand volume (m³)</td>
<td>-5.17</td>
<td>-0.47</td>
<td>0.50</td>
<td>-62.40</td>
<td>-16.00</td>
</tr>
</tbody>
</table>

Table 6 Percentage of maximum biomass and density reached by the meadows by the site of the study and time they will take before reaching their theoretical upper limit.

<table>
<thead>
<tr>
<th>Sampling sites</th>
<th>Density (%)</th>
<th>Biomass (%)</th>
<th>Time (years)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Flamingo</td>
<td>88.8</td>
<td>77.6</td>
<td>1.3</td>
</tr>
<tr>
<td>Larga</td>
<td>80.9</td>
<td>70.1</td>
<td>1.4</td>
</tr>
<tr>
<td>Petrolera</td>
<td>78.3</td>
<td>67.6</td>
<td>1.6</td>
</tr>
<tr>
<td>Paredón</td>
<td>98.6</td>
<td>85.9</td>
<td>*</td>
</tr>
<tr>
<td>Antón</td>
<td>99.6</td>
<td>86.2</td>
<td>*</td>
</tr>
</tbody>
</table>

DISCUSSION

Direct censuses of seagrass, as for any other group, are a reliable and accurate method to understand the current state of a population. However, they can be costly, time-consuming, and hence, in many occasions unlikely to be repeated over extended periods [41]. Alternatively, reconstruction methods such as the ones explored in this study can be implemented to overcome knowledge gaps in the former state of seagrasses. As shown by the results herein, both methods coincided in their ability to calculate vertical growth rates but differed in the measures of mortality and recruitment. Such outcomes highlight that although reconstruction methods can provide insight on seagrasses dynamics, censuses should still be conducted to obtain accurate demographics.

The reconstructive measure obtained by graphically representing the sequence of interannuals for each shoot showed that the biannual leaf production cycle followed a pattern of seasonal changes associated with the length of rhizome segments. The PI determined for the meadows in this study shows the lowest values (i.e., approximately half of the mean values reported for the species [25] [42] [43] [39]). These low values reflect a rapid growth rate of the meadows of Cayo Coco, coinciding with exceptional low PI values (i.e., four days) reported in some seagrass meadows in Florida after analyzing offspring surviving an extreme mortality event [43].

The total seagrass biomass calculated for all stations showed similar to that in other meadows of T. testudinum studied in Cuba [18] [44] [45], as well within the Caribbean Sea [46]. In general, the annual leaf production for T. testudinum has been estimated between 12 and 31 leaves per shoot per year [30]. Here we found that shoots at Cayo Coco have a high annual leaf production, which exceeds the average production reported for the species [13] [3]. This high leaf production is related to the vertical growth of the shoots, which varies in response to the degree of their burial [42].

Concurrently, the vertical growth of shoots found in the experimental meadows is among the highest in the literature [23]. The values determined herein are five times greater than the average for the species and the maximum vertical growth reported to date. Similar values coincide with the effects of Hurricane Gilbert in Mexico [47]. In addition to natural and anthropogenic driven events in other regions of the Caribbean [25], Mediterranean Sea [39], and South Asia [48] in which heavy loads of sediment were transported to the meadows causing burial of seagrasses, which lead to higher growth rates than average.

Reconstruction methods used to calculate vertical growth have shown to be the key to highlight seagrasses as biological tracers of sediment movement over the meadows [27]. Results showed a relationship between the foliar biomass of the meadows and the sediment dynamics of the beach adjacent to the study sites. Both biomass and vertical growth were greater in meadows where the beach had a larger volume difference of sand within a year. It is possible that the net loss of sand calculated on adjacent beaches deposited onto the meadows. The meadows of T. testudinum studied herein are located within a pre-reef lagoon. The most extensive meadows in Paredón and Antón stations are located towards the East of Cayo Coco, where the reef separates even more from shore. Their extension and
maximum depth are limited by the availability of suitable substrate and not by light limitations. Hence, sediment deposition could provide a new suitable substrate for colonization, coinciding with the greater shoot density, biomass, and vertical growth observed at these sites, particularly at Paredón.

Demographic indicators derived from the retrospective methods show meadows having a net loss driven by mortality events occurring 3–4 years before this study. Similar values have been reported in meadows from the Mexican Caribbean that have suffered a considerable loss due to hurricanes (49) or by massive mortality events caused by fungal spread outs covering leaves (50). However, the mortality rates obtained by the direct census method are much lower than the estimates for previous years. The census also revealed a positive net population growth indicating that the meadows in Cayo Coco are currently expanding. These meadows were likely affected by climate-driven events like hurricanes and storms typical of Cuba, which deposited sediments onto the meadows causing a temporary increase in mortality rate but now facilitating their recovery and explanation.

According to the allometric relationship between shoot biomass and their spacing (Figure 5), Cayo Coco meadows still have the potential to increase their density and biomass. Given their architecture and average demographic status of the meadows, they could reach their maximum biomass and density in 1.3-1.6 years, if current environmental conditions remain stable without major disturbance events increasing mortality events. These results predict a rapid recovery period of 2-4 years in the event of a major natural sand burial event. Overall, results suggest that meadows at Cayo Coco were significantly buried in recent years and that burial led to high mortality. In turn, seagrass offspring responded with increased vertical growth compensating mortality and allowing recovery. The current mortality rates probably relate to relatively stable environmental conditions, allowing meadows to expand and increase density.

Moreover, given the growth rates calculated, it appears that meadows at Cayo Coco completely recovered only one or two years after the hypothesized major burial event. The combination of reconstructive and direct demographic studies has complementary application to determine the status of populations.

CONCLUSION

Differences between mortality and recruitment indicate the robustness of direct over indirect methods. Direct censuses are therefore very effective in assessing severe weather events such as hurricanes and storms.

On the other hand, reconstructive methods are preferable to explore the growth dynamics of Thalassia testudinum because they are less laborious and do not need regular visits to areas of interest.

This study provides with a better understanding of the meadows ecology to be applied by the corresponding Cuban agencies to better allocate efforts in conducting both direct and indirect monitoring methods with could vary in frequency to maximize the use of resources and still obtain long term and reliable data about the status of Thalassia testudinum meadows in the island.

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