David Tomasko, Stephen Crooks and Doug Robison

ABSTRACT

As of 2012, there were an estimated 14,243 ha of seagrass meadows in Tampa Bay. Seagrass meadows are the dominant blue carbon habitat in Tampa Bay, compared to the estimated 6,127 ha of mangroves and 1,779 ha of saltmarsh. However, and unlike mangroves and saltmarshes, the entirety of carbon fixation, growth and decay in seagrass meadows occurs in a submerged environment. While rates of primary production in seagrass meadows rank among the highest for any ecosystem on the planet, the organic content of sediments below seagrass meadows is typically much lower than the organic content of soils associated with mangroves and saltmarshes. This paper compares bay-wide estimates of primary production of seagrass meadows in Tampa Bay to estimates of carbon sequestration via sediment burial alone. The much greater rates of primary production found, compared to rates of carbon sequestration via burial, leads to two main conclusions – either sequestration can occur via pathways other than burial alone, or a much smaller percentage of assimilated carbon is sequestered by seagrass meadows, compared to other blue carbon habitats. Based on a combined estimate of both physical and chemical sequestration processes and pathways, the seagrass meadows of Tampa Bay appear to be able to sequester approximately 41,731 Mg C / yr, which approximates the annual carbon output of ca. 32,000 typical cars.

INTRODUCTION

Recently, the term “blue carbon” has gained significant levels of attention by marine researchers and resource managers. Blue carbon refers to that amount of carbon storage and sequestration that is associated with marine ecosystems. Tampa Bay is one of four members of the EPA’s National Estuary Program to contain three major blue carbon habitats: salt marshes, mangroves, and seagrass beds (Russell and Greening 2015).

More than 30 years ago, seagrass meadows were suggested to be an important carbon sink that could mitigate some of the impacts of anthropogenic CO2 loads to the atmosphere (Smith 1981). The idea that seagrass meadows could be an important component of carbon sequestration is in part due to the documentation of very high levels of primary production, as early researchers noted that primary production rates of seagrass meadows “…can rival the most productive agricultural areas” (Westlake 1963 as cited by Zieman and Wetzel 1980). While carbon storage values and sequestration rates are fairly well documented for some blue carbon habitats, sequestration rates for seagrass meadows need to take into account that seagrass meadows are fully submerged habitats, and the fate of
assimilated carbon is likely more strongly influenced by water chemistry than is the case with salt marshes and mangroves.

This paper summarizes the uncertainties that exist related to carbon sequestration rates for seagrass meadows by comparing bay-wide estimates of carbon sequestration against each other using different assumptions available in peer-reviewed literature. In addition, these separately derived carbon sequestration estimates were then compared against a bay-wide estimate of the potential amount of annual carbon assimilation via seagrass throughout Tampa Bay. The literature related to carbon assimilation rates was also compared to a short-duration experiment conducted with the species *Thalassia testudinum*, to determine if literature-based estimates might over or under estimate bay-wide and annualized primary production estimates, based on expectations of variability due to water depth and season. Finally, discrepancies between an estimate of bay-wide carbon assimilation and various literature-derived carbon sequestration rates are discussed as to how such differences can be resolved in the future.

**MATERIALS AND METHODS**

*Developing literature-based carbon assimilation rate estimates for seagrass*

Estimates of primary production rates of seagrass meadows date back more than 100 years, when Peterson (1918, as cited in Zieman and Wetzel 1980) estimated production rates of *Zostera marina* in Danish waters. Rates of primary production have typically been measured either through changes in above-ground biomass over time or rates of carbon uptake for all the major species of seagrass found in Tampa Bay. A summary of area-normalized rates of carbon assimilation, by species, was developed based on literature for those genera, if not species, that are found in Tampa Bay. For those studies where production was originally expressed in units of grams dry weight, rather than grams of carbon, we assumed a carbon content of 35 percent of dry weight to convert units of dry weight to units of carbon, as per Fournqurean et al. (2012). When values were not available on a yearly basis, an annual estimate was derived based on the average of all available values (sometimes estimated from graphs if no data were shown in tabular form) for each report. For most of the literature, it appears that the primary method of data collection was such that production rates are derived based on changes in above-ground biomass overtime, which likely underestimates total production.

For the species *S. filiforme*, prior work has shown that perhaps 60 percent of above-ground productivity is exported to other locations (Zieman 1980). For the purposes of this study, that amount of exported productivity is not counted, as the purpose here is to estimate the potential for carbon sequestration within Tampa Bay itself. Export rates of 1 percent were applied to areal production rate estimates for both *Halodule wrightii* and *Thalassia testudinum*, consistent with estimates from Zieman and Wetzel (1980).
The area-normalized net primary production rate estimates in the literature vary substantially between species. To develop bay-wide estimates of net primary production, seagrass acreage estimates for different bay segments were combined with transect data to come up with estimated coverage, by species, for each major segment of Tampa Bay. Species composition in each of the major bay segments was estimated using data within Avery and Johansson (2001) who recorded information on the species distribution along each of 61 seagrass monitoring transects throughout Tampa Bay. Transects were located in Hillsborough Bay (11), Old Tampa Bay (12), Middle Tampa Bay (13), Lower Tampa Bay (14) and Boca Ciega Bay (11). For those transects where seagrass was encountered, the percent frequency of occurrence for each species was calculated and that frequency of occurrence was then multiplied by the acreage of seagrass per bay segment for the year 2012. For example, if the combined transects in Old Tampa Bay had H. wrightii occurring 75 percent of the time when seagrass was found, and T. testudinum occurring 25 percent of the time when seagrass was found, and the total acreage of seagrass was 500 acres, then it would be estimated that H. wrightii meadows would account for 375 acres of seagrass (0.75 x 500 acres) and T. testudinum would account for 125 acres of seagrass (0.25 x 500 acres). These acreage estimates for each bay segment were then multiplied by the species-specific primary production estimate, and the values for each species, for each bay segment, were then summed to develop a bay-wide primary production estimate for all species combined.

Field study to measure seagrass carbon assimilation rates

To verify the appropriateness of the literature-based carbon assimilation rates, a field study was conducted during the period of May11 to May 22, 2015. The field study was conducted at two locations, a T. testudinum meadow on the east side of Old Tampa Bay south of the Courtney Campbell Causeway (site OTB; 27° 58’ north latitude, 82° 33’ west longitude) and a second T. testudinum meadow offshore of Ft. De Soto Park (site LTB; 27° 38’ north latitude, 82° 42’ west longitude). The two sites were chosen to represent locations with both low (OTB) and high (LTB) sediment carbonate contents (data from USGS 2007).

Study sites were at the deep edge (where shoots occupied approximately 10 percent of 10 cm by 10 cm cells in a 1 square meter quadrat), the shallow edge (where T. testudinum was at 100 percent coverage but where shallower depths were not occupied by T. testudinum) and at a mid-depth, approximately half way (distance) between the shallow and deep edges.

At each depth, above-ground primary production was estimated using the needle-marking technique, as in Dawes and Tomasko (1988) Tomasko et al. (1996) and Tomasko and Hall (1999). This technique involves marking seagrass blades (n =5) with a hypodermic needle, and recording the amount of blade material produced over time based on the upward displacement of blades compared to a reference point on the seagrass shoot. Shoot densities were enumerated in 10 replicate 25 cm by 25 cm quadrats. Areal primary production rate estimates were derived by
taking the shoot-specific production rate estimates and multiplying them by shoot densities normalized to a square meter. Due to either vandalism or other factors, the marked shoots at the shallow edge in Old Tampa Bay could not be found. Different shoots were used to estimate biomass per shoot, and per shoot biomass was multiplied by the mean turnover rate at the other two locations in Old Tampa Bay to derive a productivity estimate for the shallow edge at that location.

A previously developed regression between blade area and dry weight (Prado and Heck 2011) was combined with leaf carbon content estimates from Fourquarean et al. (2012) to derive carbon assimilation rate estimates in units of g C m\(^{-2}\) d\(^{-1}\).

**Developing literature-based carbon sequestration rates for seagrass**

Bay-wide estimates of carbon sequestration were developed based on an approach outlined in Russell and Greening (2015). In that paper, the authors used bay-wide estimates of seagrass coverage and combined that information with literature-derived estimates of carbon sequestration rates for seagrass. Using those two parameters, estimates of carbon sequestration across the entire bay were then developed (Russell and Greening 2015). For purposes of the assessment outlined in this memorandum, the bay-wide seagrass coverage estimate for the year 2012 of 14,243 ha (35,194 acres) was used, to allow comparison with other blue carbon sequestration amounts listed in Russell and Greening (2015).

**RESULTS**

**Literature-based carbon assimilation rate estimates**

A summary of area-normalized rates of carbon assimilation for various species found in Tampa Bay is shown in Table 1. The values in Table 1 are the arithmetic averages of all the annual estimates for each species from each report cited. The rate estimate from Chiu et al. (2013) is for the species *T. hemprichii*, rather than *T. testudinum*, the species found in Tampa Bay.
Table 1 – Literature-derived area-normalized rates of carbon assimilation by species.

<table>
<thead>
<tr>
<th>Species</th>
<th>Annual net primary production estimate (g C m⁻² yr⁻¹)</th>
<th>Studies used to develop estimate</th>
</tr>
</thead>
<tbody>
<tr>
<td>Syringodium filiforme</td>
<td>292</td>
<td>Zieman and Wetzel (1980)</td>
</tr>
</tbody>
</table>

Using the approach outlined above, the species composition estimates by bay segment were then compiled for the bay as a whole for the year 2012. The amount of seagrass coverage, bay-wide and by species, is estimated as: H. wrightii – 7,297 ha, T. testudinum – 4,598 ha, Syringodium filiforme – 2,126 ha, Halophila engelmannii – 202 ha, and Ruppia maritime – 19 ha.

These bay-wide estimates of seagrass coverage, by species, were than multiplied by the primary productivity estimates in Table 1 to develop a carbon assimilation rate estimate. This bay-wide estimate came to 89,255 Mg C per year, or 89 million kg C per year.

Field study of seagrass carbon assimilation rates

Table 2 summarizes results of the seagrass primary production field study, in terms of shoot density, biomass per shoot, and leaf turnover rate. Shoot densities are shown as estimates per square meter, based on multiplying the mean value of n=10 recordings of shoot density per 25 cm by 25 cm quadrat.
Table 2 – Results from shallow, mid and deep depths of *Thalassia testudinum* in Old Tampa Bay and Lower Tampa Bay. Shoot density is represented as mean per square meter, based on 25 cm by 25 cm quadrats (n = 10). Other estimates are based on n = 5. Turnover rates could not be directly measured at Old Tampa Bay shallow depths (see text for explanation).

<table>
<thead>
<tr>
<th>Site</th>
<th>Depth</th>
<th>Shoot density (no. / m²)</th>
<th>Biomass per shoot (mg dw / shoot)</th>
<th>Turnover rate (percent / d)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean</td>
<td>Mean</td>
<td>Std. dev.</td>
<td>Mean</td>
</tr>
<tr>
<td>Old Tampa Bay</td>
<td>Shallow</td>
<td>488</td>
<td>190.0</td>
<td>66.4</td>
</tr>
<tr>
<td>Old Tampa Bay</td>
<td>Mid</td>
<td>77</td>
<td>67.1</td>
<td>42.6</td>
</tr>
<tr>
<td>Old Tampa Bay</td>
<td>Deep</td>
<td>43</td>
<td>64.7</td>
<td>26.2</td>
</tr>
<tr>
<td>Lower Tampa Bay</td>
<td>Shallow</td>
<td>454</td>
<td>516.6</td>
<td>125.6</td>
</tr>
<tr>
<td>Lower Tampa Bay</td>
<td>Mid</td>
<td>384</td>
<td>237.0</td>
<td>53.7</td>
</tr>
<tr>
<td>Lower Tampa Bay</td>
<td>Deep</td>
<td>19</td>
<td>202.5</td>
<td>52.4</td>
</tr>
</tbody>
</table>

Shoot densities and biomass per shoot declined from shallow to deep edges, as had been previously found for *T. testudinum* meadows in Tampa Bay (Dawes and Tomasko 1988, Tomasko and Dawes 1990). However, there was no evidence of a difference in leaf turnover rates between depths. Turnover rates measured here were either similar, or slightly higher than rates previously measured in the spring to summer in both Sarasota Bay (Tomasko et al. 1996) and Charlotte Harbor (Tomasko and Hall 1999).

With leaf turnover rates being similar with depth, any differences in area-normalized primary production rates would thus reflect differences in shoot density and biomass per shoot. Converted to units of grams of carbon per square meter per day, results show that productivity often differs more with depth at a single location than it does between different locations at the same depths (Figure 1).
The mean value of above-ground primary production from both shallow locations was 2.28 g C m\(^{-2}\) d\(^{-1}\). Multiplying that rate by 365 days, the resulting annual estimate of primary production is 830 g C m\(^{-2}\) yr\(^{-1}\), similar to the literature-derived estimate for \textit{T. testudinum} of 979 g C m\(^{-2}\) yr\(^{-1}\) shown in Table 1. These results suggest that literature-based values of annual production might be over-estimates, as they are similar to values recorded here from shallow depths in the spring growing season. As production rates of \textit{T. testudinum} are known to be lower in deeper depths (Dawes and Tomasko 1988, Tomasko and Dawes 1990) and in fall to winter months (Tomasko et al. 1996, Tomasko and Hall 1999) it is thus likely that literature-based values of primary production overestimate production across the combination of depths and seasons that would be needed to develop a bay-wide and annual average value of primary production.

\textit{Literature-based carbon sequestration rates}

Literature-derived estimates of carbon sequestration rates for seagrass vary widely. In their paper, Russell and Greening (2015) used a carbon sequestration rate for seagrass meadows of 138 g C m\(^{-2}\) yr\(^{-1}\), as listed in McLeod et al. (2011). In turn, McLeod et al. (2011) developed their estimate from six published and one unpublished study on carbon burial rates in seagrass meadows.

Other researchers have published carbon sequestration rates via burial in sediments below seagrass meadows. Duarte et al. (2005) derived a global carbon sequestration rate estimate for seagrass meadows of 83 g C m\(^{-2}\) yr\(^{-1}\). In the coastal waters of Virginia, newly reestablishing seagrass meadows were estimated to sequester carbon at a rate of 38 g C m\(^{-2}\) yr\(^{-1}\) (Greiner et al. 2013) while researchers in Korea developed carbon sequestration rates for seagrass
meadows of 20 g C m\(^{-2}\) yr\(^{-1}\) (Chiu et al. 2013). Thus, if bay-wide estimates of carbon sequestration rates (amounts of carbon sequestered per year) are based on the spatial extent of meadows multiplied by area-normalized sequestration rates (g m\(^{-2}\) yr\(^{-1}\)) then bay-wide estimates could vary by a factor of nearly 7-fold, depending upon which sequestration rate estimate was used.

Figure 2 compares literature-based estimates of bay-wide carbon assimilation in Tampa Bay with literature-based bay-wide estimates of carbon sequestration via burial.

![Figure 2](image)

**Figure 2** – Comparison of bay-wide estimates of carbon assimilation vs. various literature-based and bay-wide estimates of carbon sequestration via burial. Data are in units of mega grans of carbon per year (1 mega gram = 1,000 kg).

Even if the highest literature-based carbon sequestration estimate (138 g C m\(^{-2}\) yr\(^{-1}\); McLeod et al. 2011) is used, there appears to be a much larger amount of assimilation of carbon by seagrass meadows in Tampa Bay than the amount of carbon sequestered through burial alone.
DISCUSSION

Most of the literature related to quantification of carbon sequestration benefits of seagrass meadows is based on the process of burial of fixed carbon in the sediments below these meadows (e.g., Duarte et al. 2010, Fourqurean et al. 2012, Greiner et al. 2013, McLeod et al. 2013). Using this technique, carbon sequestration is quantified as a function of the rate of accumulation of sediments over time, and the organic carbon content of those same sediments.

When annual estimates of primary production of seagrass meadows in Tampa Bay are compared to literature-based estimates of sequestration via burial alone (Figure 2) there appear to be much higher rates of carbon assimilation than even the highest estimated rate of carbon sequestration via burial. These results would suggest that there is a much larger amount of carbon assimilated by seagrass meadows than the amount of carbon sequestered by burial alone. This discrepancy is likely due to some combination of factors, such as the likelihood that literature-based estimates of annual primary production are biased on the high end, and that other mechanisms of carbon sequestration other than burial could be involved. Conversely, it could be that the vast majority of carbon assimilation via seagrass meadows is not sequestered in any way, but is recycled back into the water column or exported elsewhere, as noted for S. filiforme by Zieman and Wetzel (1980).

In seagrass meadows, carbon sequestration has been documented to occur via an alternative process to burial alone, the so-called bicarbonate pathway, described more than 30 years ago by Smith (1981). In tropical and carbonate-rich sediments, researchers have noted that the very high production rates of T. testudinum in the Bahamas did not correlate with similarly high rates of carbon accumulation in sediments. Despite very high densities of seagrass meadows, and high rates of primary production, the organic content of sediments in seagrass meadows in the Bahamas averaged less than 1 percent (Burdige and Zimmerman 2002). For seagrass meadows, the global average values of organic content of sediments listed in Duarte et al. (2010) and Fourqurean et al. (2012) are 0.7 and 1.4 percent of dry weight, respectively. In contrast, the organic content of sediments associated with mangroves and saltmarshes are typically much higher, ranging from ca. 20 to 80 percent of dry weight (when converted to similar units; Chmura et al. 2003).

For seagrass meadows, the question of “where does the fixed carbon go?” was answered in part by Burdige and Zimmerman (2002) based on the following equation:

\[ \text{CH}_2\text{O} + \text{O}_2 + \text{CaCO}_3 \rightarrow \text{Ca}^{2+} + 2\text{HCO}_3^- \]

This equation summarizes the process through which fixed carbon (CH₂O) is decomposed in carbonate sediments (CaCO₃) under conditions where sediments are oxygenated via the seagrass root/rhizome complex (O₂). The end result of this process is both free calcium ions (Ca²⁺) and previously fixed carbon now present in the form of bicarbonate ions (2HCO₃⁻). The bicarbonate portion of the world’s oceans has been referred to as a global and

In addition, Unsworth et al. (2012) have noted that the bicarbonate sequestration pathway is a mechanism though which seagrass meadows could provide a positive benefit to any nearby coral reefs, via their ability to offset impacts of ocean acidification associated with CO₂ enrichment of coastal waters. The bicarbonate sink pathway was the primary mechanism through which it is believed carbon sequestration occurs for the seagrass meadows in the Bahamas Banks (Burdige and Zieman 2002, Burdige et al 2010) and Tokyo Harbor (Isobe et al. 2012).

In Tampa Bay, recent work by Yates et al. (2015) which was conducted concurrent with the field investigation described here, determined that seagrass meadows were capable of increasing daytime pH values by 0.5 units, consistent with expectations as inorganic carbon is taken up by photosynthesis. As well, seagrass meadows were found to increase, at least locally, carbonate saturation rates in the water column, suggesting that the mechanisms involved in the bicarbonate pathway outlined by Burdige and Zimmerman (2002) could be occurring in Tampa Bay seagrass meadows.

As an initial assessment, we combined estimates of seagrass-associated rates of carbon sequestration via the physical process of burial (138 g C m⁻² yr⁻¹; MacLeod et al. 2013) with estimates of seagrass-associated rates of carbon sequestration via the chemical processes of the bicarbonate pathway (155 g C m⁻² yr⁻¹; Unsworth et al. 2012) to produce a combined carbon sequestration estimate of 293 g C m⁻² yr⁻¹. This combined sequestration estimate is nearly identical to the literature-based annualized primary production rate estimate for S. filiforme, but lower than the primary production rate estimate of H. wrightii, and substantially lower than that of T. testudinum (Table 1). Most importantly, this estimate of combined (physical and chemical) carbon sequestration pathways is not higher than the annualized primary production estimates of any of the main species of seagrass in Tampa Bay, as listed in Table 1, which would signify that sequestration was occurring in excess of assimilation (which would be difficult to interpret).

If this combined carbon sequestration rate estimate of 293 g C m⁻² yr⁻¹ is extrapolated out to the 16,307 ha of seagrass in Tampa Bay (as of 2012) then the annualized bay-wide estimate of carbon sequestration comes to 41,731 Mg C yr⁻¹. This amounts to approximately 47 percent of the estimated bay-wide annualized carbon assimilation rate for seagrass meadows of 89,255 Mg C yr⁻¹. Based on the on-line Greenhouse Gases Equivalency calculator developed by the US Environmental Protection Agency (http://www.epa.gov/energy/greenhouse-gas-equivalencies-calculator) the seagrass meadows of Tampa Bay appear capable of sequestering an amount of carbon equivalent to the carbon footprint of ca. 32,000 cars.

To increase the confidence in carbon sequestration estimates for seagrass meadows in any location, it would be useful to have multiple and site-specific data collected on sediment organic and carbonate contents within seagrass
meadows, as well as the collection of data that could be used to test for the presence of the carbonate dissolution and bicarbonate sequestration pathways outlined by Burdige and Zimmerman (2002), Burdige et al. (2012) and Unsworth et al. (2012). With these additional data, sequestration rate estimates for seagrass could be derived other than through the use of literature alone, and resource managers would have enhanced confidence in their model output for what could be a dominant blue carbon habitat, as in Tampa Bay. Without this additional data collection, the carbon sequestration values derived for seagrass meadows could vary considerably, dependent upon which study was used in calculations.

ACKNOWLEDGEMENTS

Special thanks are due to the Tampa Bay Estuary Program for funding this research, along with Restore America’s Estuaries for financial and logistical support. Discussions with Stephen Emmitt-Maddox, Kim Yates and Ed Sherwood were particularly helpful in guiding the development of the manuscript.
REFERENCES


