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Widespread recovery of seagrass coverage in Southwest Florida (USA): Temporal and spatial trends and management actions responsible for success

D. Tomasko[a,*], M. Alderson[b], R. Burnes[c], J. Hecker[d], J. Leverone[b], G. Raulerson[e], E. Sherwood[e]

[a] *Environmental Science Associates, 4200 West Cypress Street, Suite 450, Tampa, FL 33607, USA*
[b] *Sarasota Bay Estuary Program, 111 South Orange Avenue, Sarasota, FL 34236, USA*
[c] *Pinellas County Environmental Management, 22211 U.S. Highway 19, North, Clearwater, FL 33765, USA*
[d] *Charlotte Harbor Estuary Program, 326 West Marion Avenue, Punta Gorda, FL 33950, USA*
[e] *Tampa Bay Estuary Program, 263 13th Avenue, South, St. Petersburg, FL 33701, USA*

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ABSTRACT

In Southwest Florida, a variety of human impacts had caused widespread losses of seagrass coverage from historical conditions. St. Joseph Sound and Clearwater Harbor lost approximately 24 and 51%, respectively, of their seagrass coverage between 1950 and 1999, while Tampa Bay and Sarasota Bay had lost 46% and 15%, respectively, of their seagrass coverage between 1950 and the 1980s. However, over the period of 1999 to 2016, the largest of the six estuaries, Tampa Bay, added 408 ha of seagrass per year, while the remaining five estuaries examined in this paper added approximately 269 ha per year. In total, seagrass coverage in these six estuaries increased 12,171 ha between the 1980s and 2016. Focused resource management plans have held the line on nitrogen loads from non-point sources, allowing seagrass resources to expand in response to reductions in point source loads that have been implemented over the past few decades.

1. Introduction

Seagrasses have long been recognized as important coastal resources. Early studies focused on the habitat value of seagrass meadows for recreational and commercial important species of finfish and shellfish (e.g., Heck et al., 2003). Additionally, the role of seagrass meadows in stabilizing sediments and reducing rates of shoreline erosion has been noted (e.g., Fonseca and Cahalan, 1992). Seagrass meadows have also been shown to play an important role in the sequestration of carbon either through direct burial of biomass (i.e., Duarte et al., 2010; Fourqurean et al., 2012; Greiner et al., 2013; McLeod et al., 2011) or indirectly through bicarbonate sequestration (i.e., Smith, 1981; Burdige and Zimmerman, 2002; Burdige et al., 2010; Tomasko et al., 2016). The ability of seagrass meadows to offset, at least on a local to regional level, the impacts of ocean acidification, has also been documented (i.e., Unsworth et al., 2012; Yates et al., 2016) as well as other benefits (i.e., Unsworth et al., 2012; Sherwood et al., 2017).

Unfortunately, a combination of direct and indirect impacts has resulted in losses of seagrass meadows on a global scale (Orth et al., 2006; Waycott et al., 2009). Environmental degradation and seagrass loss has been documented in great detail in Botany Bay, Australia (Larkum, 1976), Cockburn Sound, Australia (Cambridge and McComb, 1984; Silberstein et al., 1986), the French Mediterranean Sea (Bourcier, 1986), and the Chesapeake Bay, USA (Kemp et al., 1983; Orth and Moore, 1984). Even in Cancun, Mexico, which was developed with a focus on water-based tourism, impacts to seagrass meadows had been documented due to degraded water quality (Reyes and Merino, 1991).

Although the scientific literature is replete with examples of environmental degradation of nearshore waters due to human activities, there are also numerous examples of environmental restoration after pollution sources have been adequately addressed. In Kaneohe Bay, Hawaii (USA) Hunter and Evans (1995) documented the degradation and eventual recovery of water quality and coral communities due to the discharge and subsequent removal of nutrient-enriched wastewater. In the coastal waters of Adelaide, Australia, Bryars and Neverauskas (2004) documented the recovery of seagrass meadows after the cessation of sewage discharges into local waters. In Gunston Cove, Virginia (USA), Jones and Krauss (2009) documented a reduction in algal blooms, a subsequent increase in water clarity, and the eventual increase in the health of aquatic communities in response to an 80% reduction in point source nutrient loads. In the Wadden Sea, van Beusekom (2010) documented improvements in water quality and the health of aquatic communities in response to nutrient load reductions over the prior 40 years.

* Corresponding author.
E-mail address: dtomasko@esassoc.com (D. Tomasko).

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In Southwest Florida, much research has focused on relationships among urban development, changing land use patterns, pollutant loads, estuarine water quality, and historical losses of seagrass coverage (i.e., Lewis et al., 1985; Lewis, 1989; Haddad, 1989). In Tampa Bay, Florida (USA), a 90% reduction in point source nitrogen loads has resulted in a substantial improvement in water quality and overall ecosystem health (e.g., Johansson, 1991; Johansson and Greening, 2000; Tomasko, 2002; Greening and Janicki, 2006; Greening et al., 2016; Sherwood et al., 2017). Similar ecosystem recovery has been documented for Sarasota Bay in response to similar reductions in point source nutrient loads (Tomasko et al., 2005).

Tomasko et al. (2005) compared and contrasted the status and trends in seagrass coverage, rainfall, and pollutant loads in four contiguous Southwest Florida estuaries – Tampa Bay, Sarasota Bay, Lemon Bay and Charlotte Harbor. At that time, recovery of seagrass coverage in Tampa and Sarasota Bays was noted, as well as the conclusion that such a trend was likely due to reductions in bay-wide nutrient loads, rather than regional trends in rainfall or other climatic phenomena. This paper provides an update on those seagrass trends with more than a decade of additional seagrass mapping efforts, and includes information on the status and trends of seagrass coverage in two additional and contiguous estuaries – St. Joseph Sound and Clearwater Harbor.

2. Materials and methods

2.1. General description of locations

For purposes of the present paper, the following estuaries will be considered: 1) St. Joseph Sound, 2) Clearwater Harbor, 3) Tampa Bay, 4) Sarasota Bay, 5) Lemon Bay, and 6) Charlotte Harbor (Fig. 1). The region "Charlotte Harbor" will include only those areas north of 26°40′ N latitude.

The climate in this portion of Southwest Florida is subtropical, with warm, wet summers and mild, dry winters. Annual average air temperatures range between 21 and 24 °C, and mean annual rainfall ranges between 136 and 144 cm year^{-1}, with more than half that amount occurring during the typical wet season of June to September (Southwest Florida Water Management District, 2018).

While in immediate proximity to one another, these estuaries vary considerably in terms of the area of open water, total watershed area, and the ratio of watershed to open water (Table 1).

Watershed sizes range from well over 5000 km^2 for both Charlotte Harbor and Tampa Bay to < 200 km^2 for both Lemon Bay and Clearwater Harbor. In terms of their open water area, Tampa Bay is nearly three times as large as Charlotte Harbor, which is more than twice the size of the next largest system – Sarasota Bay. The ratios between the watershed and the open water into which their watersheds drain differ by nearly an order of magnitude. Clearwater Harbor and Sarasota Bay have < 3 km^2 of land draining into every square kilometer of open water, while > 25 km^2 of land drain into every square kilometer of open water in Charlotte Harbor. In terms of the influence of its watershed (expressed as the watershed to open water ratio) Charlotte Harbor is four times as affected as Tampa Bay, which is more than twice as affected by its watershed as Sarasota Bay and Clearwater Harbor.

2.2. Seagrass mapping techniques

Since 1988, estimates of seagrass area, or coverage, have been derived from photointerpretation of aerial imagery acquired under strict protocols (Tomasko et al., 2005). However, resource managers also desired estimates of coverage from before 1988. In St. Joseph Sound, Clearwater Harbor, Tampa Bay and Sarasota Bay, seagrass maps have been generated from aerial imagery collected over a series of flights from 1948 to 1950 and are referred to as "1950" seagrass maps. Tampa Bay and Charlotte Harbor also have seagrass maps for the year 1982. Based on assessments of water quality and pollutant loads, 1950 is considered to represent reference conditions for seagrass distribution, as it appears that seagrass meadows were widely distributed throughout the region (and minimally impacted at that time). In contrast, the years 1982 or 1988 represent degraded conditions, as pollutant loads were at or close to their highest levels and water quality was typically much worse (at least in Tampa and Sarasota Bays) than it was in 1950 (i.e., Tomasko et al., 2005; Greening et al., 2016). For Charlotte Harbor and Lemon Bay, 1950 seagrass estimates were viewed as potentially suspect based on the difficulty of photointerpretation in some areas.

Seagrass maps for 1950 and 1982 were previously produced via photointerpretation of 1:24,000 scale aerial photographs (Tampa Bay Regional Planning Council, 1986; Haddad, 1989). Starting in 1988, the SWFWMD has managed a long-term seagrass mapping program for Tampa Bay, Sarasota Bay, Lemon Bay and Charlotte Harbor. In 1999, the mapping effort was expanded to cover St. Joseph Sound and Clearwater Harbor. The details of the seagrass mapping techniques are discussed in Tomasko et al. (2005) and Sherwood et al. (2017). Starting in 2004, aerial photography and subsequent photointerpretation transitioned from scanned true colour film media to digitally-acquired aerial imagery.

Since 1988, approximately biennial seagrass coverage estimates have been produced based on imagery acquired during the autumn to winter months, as this is the typical dry season in Southwest Florida. The dry season, with lower runoff, is associated with a generalized increase in water clarity in coastal waters, allowing for the acquisition of imagery more likely to be able to pick up the offshore, deeper margins of existing seagrass meadows. Photographic signatures are mapped using two broad categories, patchy and continuous. Polygons mapped as patchy seagrass have seagrass in approximately 25 to 75% of their boundaries, while polygons categorized as continuous have > 75% seagrass coverage within their boundaries. Up to 2012, the minimum mapping unit was set at approximately 0.2 ha in size. Due to the move to digital imagery, this minimum mapping unit was reduced to 0.1 ha starting in 2014.

After the acquisition of aerial photography, field work is conducted to improve the photointerpretation, with special attention focused on areas where the signature is not particularly clear as to whether it represents seagrass, macroalgae, or a combination of the two. After the maps have been generated, the final product is not accepted unless there is at least 90% concurrence of seagrass presence between field ground-truthed points randomly selected from within the created seagrass maps and the classification of those locations. The coverage of more diminutive species of seagrass, such as species within the genus Halophila, are not captured through the use of aerial photography. Fortunately for this effort, species of Halophila are only rarely encountered in local waters, as documented in Tampa Bay (Tomasko et al., 2016).

2.3. Rainfall

The SWFWMD collects and/or compiles rainfall data from 370 gage sites throughout its approximately 28,000 km^2 jurisdictional area, which includes all of the estuaries in this study. Data are available for various periods of record, although most regions have one or more rainfall gage sites that date back to 1915. Rainfall data were combined for all stations throughout each estuary's watershed. For St. Joseph Sound and Clearwater Harbor, rainfall data from the Tampa Bay watershed were used, as the rainfall record is more complete for that region. For Sarasota and Lemon Bays, rainfall data were combined, since these watersheds are relatively small, compared to Tampa Bay and Charlotte Harbor. For Charlotte Harbor, rainfall data were combined from throughout the Peace River watershed, which is the largest (ca. 6000 km^2) source of freshwater inflow to the estuary.

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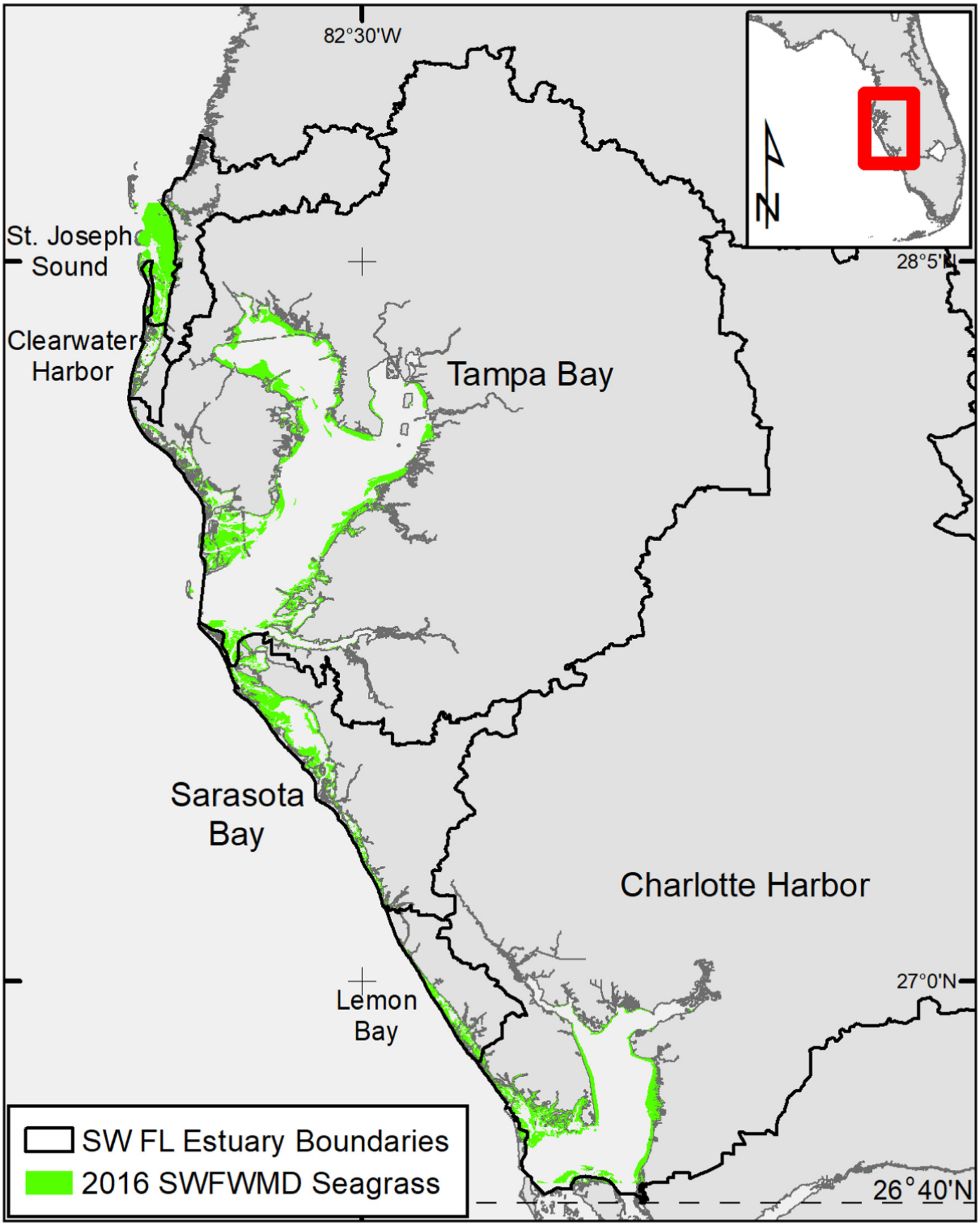

Fig. 1. Overview map showing southwest Florida estuarine boundaries and 2016 estimated seagrass coverage (Data Sources: US Geological Survey and Southwest Florida Water Management District).

2.4. Pollutant loading models

In Clearwater Harbor, recent increases in seagrass coverage have co-occurred with reductions in concentrations of Total Nitrogen (TN) in the major inflows, while there was no evidence of a reduction in concentrations of Total Phosphorus (TP) over the same time period (Janicki Environmental and Atkins, 2011). In Tampa Bay, Johansson (1991) found that nitrogen, rather than phosphorus, was the nutrient that most strongly influenced phytoplankton growth. In both Sarasota Bay (Tomasko et al., 1996) and Lemon Bay (Tomasko et al., 2001) the spatial and temporal patterns of seagrass biomass and productivity were both correlated with watershed-wide nitrogen loads. And in Charlotte Harbor, manipulative studies (Montgomery et al., 1991) found that nitrogen, not phosphorus, was the nutrient that limited phytoplankton growth. Consequently, pollutant loading models for these six estuaries focus on nitrogen as the primary (i.e., limiting) nutrient of concern.

Nitrogen loading estimates for Tampa Bay, Sarasota Bay, Lemon Bay, and Charlotte Harbor combine measured nitrogen loads from gaged locations with estimated loads from difficult to quantify sources. The loading model for St. Joseph Sound and Clearwater Harbor used estimates of surface water runoff and values of TN and TP that were

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Table 1
Estimates of open water (km^2), watershed (km^2) and the ratio between watershed to open water for St. Joseph Sound, Clearwater Harbor, Tampa Bay, Sarasota Bay, Lemon Bay, and Charlotte Harbor. Data from St. Joseph Sound and Clearwater Harbor are from Janicki Environmental, Inc., and Atkins (2011). Data from Tampa Bay are from Pribble et al. (2001). Data from Sarasota Bay are from Tomasko et al. (1996). Data from Lemon Bay and Charlotte Harbor are from Squires et al. (1998).

Estuary	Watershed (km^2)	Open water (km^2)	Watershed: open water ratio
St. Joseph Sound	342	73	4.7
Clearwater Harbor	109	39	2.8
Tampa Bay	5896	959	6.1
Sarasota Bay	389	135	2.9
Lemon Bay	154	31	5.0
Charlotte Harbor	8549	337	25.4

informed by long-term trends in water quality from monitoring stations. The water quality data in contributing tributaries was from the years 1992 to 2009. Based in part on extrapolations of water quality data to earlier years, the TN loads to St. Joseph Sound and Clearwater Harbor were estimated for the years 1985 to 2008 (Janicki Environmental and Atkins, 2011).

For Tampa Bay, approximately 57% of the watershed is gaged for both flow and water quality, allowing for direct estimates of loads. However, much of the developed portions of these same watersheds drain directly to the bay, downstream of any monitoring stations. In ungaged locations, TN loads from stormwater runoff were estimated using predictions based on rainfall, land use, soils, and seasonal land-use-specific water quality concentrations (Pribble et al., 2001). These nutrient load estimates are updated on a regular basis, to provide guidance for the management of Tampa Bay (e.g., Janicki Environmental Inc., 2017).

In contrast, the entirety of stormwater-related nitrogen load estimates for Sarasota Bay (PBS&J, 2009) and Lemon Bay (Tomasko et al., 2001) are from models of non-point source loads associated with various land use types, due to the paucity of gaged flows.

The majority of the nutrient load to Charlotte Harbor comes from the Peace River watershed, and 87% of the Peace River's watershed is gaged (Squires et al., 1998) a much higher percentage than the other five estuaries. Since so much of the Peace River is gaged, TN load comparisons shown here for Charlotte Harbor are based solely on the gaged portions of the Peace River. At locations where flows are directly measured, water quality samples have been collected on a monthly or bi-monthly basis for over 30 years. Based on this data set, annual load estimates from the Peace River were derived by multiplying monthly average flow rates (available online from the USGS) by monthly water quality data (e.g., mg TN/liter) and summing monthly load estimates for the entire year. Using this approach, TN loads from the 7-year period of 1985 to 1991 (Squires et al., 1998) were then directly compared to TN load estimates from the same watershed over the 7-year period of 2009 to 2015.

In addition to stormwater runoff, other pollutant sources included in these models are point sources (both industrial and domestic wastewater treatment plants), atmospheric deposition of nitrogen onto open water, baseflow (i.e., uncontaminated groundwater), septic tanks, and, in the case of Tampa Bay, material losses from fertilizer processing and transport facilities along the shoreline. For point source load estimates, values for individual facilities are calculated from measurements of discharge rates and concentrations required for permit compliance (e.g., Pribble et al., 2001; Squires et al., 1998). Point source loads are summed for each estuary.

In Tampa Bay, atmospheric deposition of nitrogen to the open waters of the bay was calculated by multiplying the volume of precipitation onto the bay by nitrogen concentrations in rainfall, and by direct measurements of both wet and dry deposition (Poor et al., 2001). In both Sarasota and Lemon Bays, estimates are for wet deposition only (Tomasko et al., 1996; Tomasko et al., 2001, respectively).

Baseflow (uncontaminated groundwater contributions) and septic tank system loads are estimated using various algorithms to quantify their impacts (e.g., Squires et al., 1998; Tomasko et al., 2001). These techniques all require significant extrapolations and have not yet been locally verified in each system.

For St. Joseph Sound and Clearwater Harbor, annual load estimates are available for the years of 1985 to 2008. For Tampa Bay, nitrogen load estimates exist for the years 1938, 1976, and annually from 1985 through 2016 (e.g., Pribble et al., 2001). The year 1938 is considered a reference condition, while 1976 is indicative of the most degraded conditions that Tampa Bay had experienced (Johansson and Greening, 2000; Greening and Janicki, 2006). For Sarasota Bay, nitrogen load estimates are for the years, 1890, 1988 and 1990 (PBS&J, 2009). Estimates for 1890 are for a reference condition, while 1988 is considered to be indicative of the most degraded conditions for Sarasota Bay (Kurz et al., 1999). Nitrogen load estimates for Lemon Bay are for the years 1850 and 1995 (Tomasko et al., 2001), while estimates for Charlotte Harbor are shown here for the gaged portions of the Peace River, with load estimates for the years 1985 to 1992 (Squires et al., 1998) and 2009 to 2015 (D. Tomasko, unpublished data).

3. Results

3.1. Seagrass mapping

Table 2 contains results from seagrass mapping efforts for the six estuaries. Estimates of coverage vary between the systems, and estimates for historical conditions are more reliable in some waterbodies than in others. For example, while there are estimates for the period of “1950” for Charlotte Harbor, that system has always had lower water clarity than adjacent systems, in part because of its very high watershed to open water ratio (Table 1).

The years with the lowest seagrass coverage (for those years with estimates) are 2006 for St. Joseph Sound, 1999 for Clearwater Harbor, 1982 for Tampa Bay, 1988 for Sarasota Bay, 2001 for Lemon Bay, and 1992 for Charlotte Harbor. St. Joseph Sound and Clearwater Harbor lost approximately 24 and 51%, respectively, of their seagrass coverage between 1950 and 1999. Over the same time period, Tampa Bay lost approximately 47% of its seagrass coverage, while Sarasota Bay lost 15% of its seagrass coverage.

Table 2
Seagrass coverage (ha) for St. Joseph Sound (SJS), Clearwater Harbor (CLWR), Tampa Bay (TB), Sarasota Bay (SB), Lemon Bay (LB), and Charlotte Harbor (CH). Estimates of historical (ca. 1950) seagrass coverage from Janicki Environmental (2010). Other data from Southwest Florida Water Management District.

Year	SJS	CLWR	TB	SB	LB	CH	Total
1950	6190	2433	16,357	4142			
1982			8761			7402	
1988			9424	3501	1054	7451	
1990			10,210				
1992			10,424			7247	
1994			10,736	3749	1066	7537	
1996			10,901		1053	7784	
1999	4703	1198	10,054	3742	1049	7355	28,101
2001	4316	1345	10,555	3715	1046	7387	28,363
2004	4739	1383	10,938	3741	1113	7343	29,257
2006	4179	1792	11,452	3988	1098	7432	29,941
2008	5043	1934	11,998	5116	1158	7031	32,279
2010	5118	1887	13,313	5136	1229	7328	34,010
2012	5169	1727	14,019	5094	1256	7653	34,918
2014	5229	1724	16,307	5378	1323	8052	38,012
2016	5198	1721	16,857	5451	1304	8207	38,738

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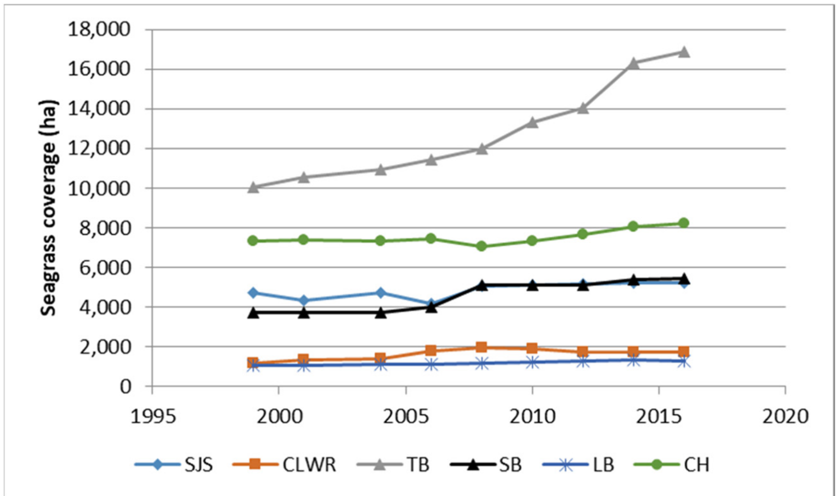

Fig. 2. Seagrass coverage (ha) in St. Joseph Sound (SJS), Clearwater Harbor (CLWR), Tampa Bay (TB), Sarasota Bay (SB), Lemon Bay (LB), and Charlotte Harbor (CH) from 1999 through 2016. Data from Southwest Florida Water Management District.

In terms of the severity of seagrass losses from historical conditions, Sarasota Bay had the least significant losses, followed by St. Joseph Sound. Tampa Bay and Clearwater Harbor both had losses of historical seagrass in excess of 40%. However, between 1982 and 1999, seagrass coverage in Tampa Bay had already increased by 15%, while coverage in Sarasota Bay had increased by 7% between 1988 and 1999.

Overall, while the six estuaries lost historical seagrass coverage between 1950 and the late 1990s, recovery had already begun in two systems (Tampa Bay and Sarasota Bay) by 1999. By 2016, Tampa Bay's mapped seagrass exceeded the historical coverage estimate. In Sarasota Bay, seagrass coverage had already exceeded 1950s estimates in 2008. Clearwater Harbor does not yet have the coverage of seagrass it had in 1950, but its recent coverage (i.e., 2012 to 2016) is the highest amount recorded over the past 17 years.

It has only been since 1999 that concurrent estimates, using the same methodologies, are available for all six estuaries (Fig. 2). When results are compared from 1999 to present, the positive trend in seagrass coverage in Tampa Bay dominates the patterns for the other five systems, in part because it consistently has had more coverage than the other systems, which is due in part to Tampa Bay having nearly three times as much open water as the next largest estuary, Charlotte Harbor.

The influence of Tampa Bay's large – and increasing – seagrass coverage makes it difficult to see that seagrass recovery is also occurring in systems other than Tampa Bay. To determine if the trend in seagrass recovery was different between Tampa Bay and the other five estuaries, coverage was plotted as the average rate of increase (ha yr^1) for the period 1999 to 2016 for Tampa Bay alone, and the five estuaries combined with and without Tampa Bay (Fig. 3).

The results shown in Fig. 3 show that Tampa Bay has added about 408 ha per year of seagrass, over the period of 1999 to 2016. During that same period of time, the other five estuaries, which have more seagrass than Tampa Bay alone, had seagrass increases of approximately 269 ha per year, a lower rate than was found for Tampa Bay. Combined, seagrass coverage in all six estuaries increased at a rate of approximately 677 ha per year between 1999 and 2016. While the results indicate that the rate of increase is greater in Tampa Bay than the other five systems, there is also clear evidence that regional improvement in seagrass coverage extends to all six of these Southwest Florida estuaries.

It appears that while seagrass coverage in Tampa Bay has increased at a fairly steady rate, many of the estuaries had increases in coverage that varied over time. Fig. 4 plots seagrass coverage from all six estuaries, comparing values for each mapping event after 1999 to the amount of seagrass mapped in 1999.

Results shown in Fig. 4 show that the pattern of recovery differs between the six systems. For example, the biggest increase in seagrass coverage for Clearwater Harbor occurred between 2004 and 2006, an increase of 30% in just two years. In Sarasota Bay, seagrass coverage increased by 28% in the two years between 2006 and 2008. In Tampa Bay, the rate of increase has been more constant over time, with increases of around 10% between mapping events, with the exception of a 16% increase between 2012 and 2014.

Seagrass mapping techniques have varied over time, with the biggest change being the conversion to digital imagery in 2004. The finding that the largest improvements in seagrass coverage occurred at different times for Clearwater Harbor, Sarasota Bay and Tampa Bay suggest that the increases are not due to a single change in climatic conditions, or the introduction of a single modification to the mapping techniques (as was done in 2004). Instead, it appears that seagrass recovery has proceeded at slightly different timescales for the six estuaries examined here. Overall, seagrass coverage improved by 10,637 ha between 1999 and 2016, an increase of 38%. The 10 years between 2004 and 2014 were associated with the majority of the recovery noted here, with a 32% improvement in seagrass coverage across the six estuaries, an increase of 8755 ha.

The distribution of seagrass meadows across the six estuaries has changed over time. In 1999, 62% of seagrass coverage was found in Tampa Bay and Charlotte Harbor, with 30% of seagrass coverage in St. Joseph Sound and Sarasota Bay. The remaining 8% of seagrass coverage was evenly split between Clearwater Harbor and Lemon Bay (Fig. 5).

By 2016, 65% of seagrass coverage was found in Tampa Bay and Charlotte Harbor, with 27% of seagrass coverage in St. Joseph Sound and Sarasota Bay. The remaining 8% of seagrass coverage was nearly evenly split between Clearwater Harbor and Lemon Bay. Total seagrass coverage for all estuaries increased from 28,101 to 38,738 ha from 1999 to 2016 (Table 2). The increasing dominance of seagrass coverage in Tampa Bay is not because of declines in coverage in the other five systems, but because the rate of increase in Tampa Bay outpaced the other estuaries (Fig. 3).

3.2. Rainfall

From 1982 to 2016, there was no monotonic trend in rainfall in any of the estuaries' watersheds (Fig. 6).

As shown in Fig. 4, it appears that the largest increases in seagrass coverage occurred from 2006 to 2016. As seagrass coverage integrates water quality conditions for longer periods of time than a single year, the rainfall data were also examined over the period with consistent

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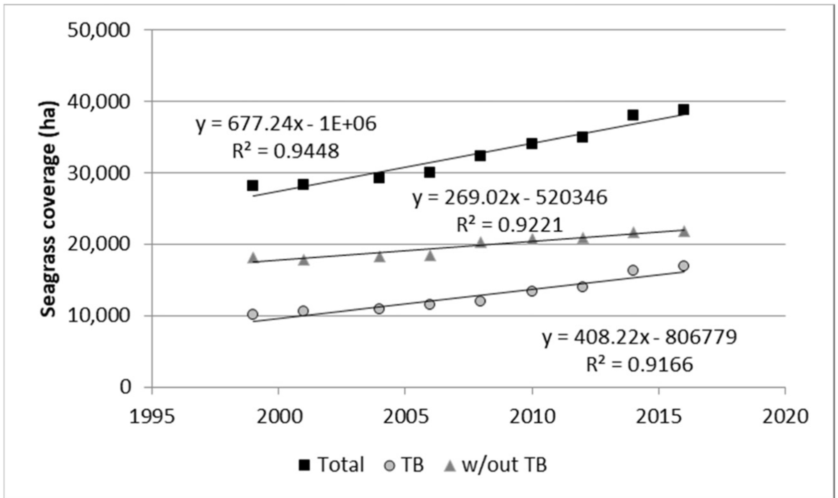

Fig. 3. Trends in seagrass coverage from 1999 through 2016 for all six estuaries combined, Tampa Bay alone, and the five estuaries other than Tampa Bay. Lines represent statistically significant best fit relationships ($p < 0.05$) between years and seagrass coverage.

mapping techniques, 1999 to 2016 (Fig. 7).

The rainfall data shown in Fig. 7 show a pattern wherein the latter years represent a period of below-average rainfall, with the rainfall deficit varying spatially. In the Tampa Bay/Coastal Areas watershed, 7 of the past 12 years had annual rainfall below the long-term average. In the Sarasota/Lemon Bay watershed, annual rainfall was below the long-term average for 10 of the last 12 years, while in the Peace River watershed, annual rainfall was below the long-term average in 9 of the last 12 years. In all three watersheds, the period of 2005 to 2016 had generally lower levels of rainfall than the long-term average, yet the overall trend was of increasing amounts of rainfall in all three watersheds.

3.3. Pollutant loads

Pollutant loads over time for each system are summarized in Table 3.

In St. Joseph Sound, annual TN loads did not show any temporal patterns, and point source discharges averaged only 2% of the estimated TN loads. Loads of TN to St. Joseph Sound ranged from ca. 79,000 to ca. 333,000 kg TN $year^{-1}$ from 1985 to 2008. The two years with the highest TN loads to St. Joseph Sound were 2004 and 1998, which respectively represent the years when Florida was hit with four hurricanes (Charley, Frances, Ivan and Jean) and the very wet 1997 to 1998 El Niño. The lowest TN loads to St. Joseph Sound during those 24 years were 1989 and 2007.

In Clearwater Harbor, annual TN loads over the 24-year period of 1985 to 2008 ranged between approximately 50,000 and 222,000 kg TN per year. Elevated TN loads were seen during El Niño years and the 2004 hurricane season, but there was no obvious trend in TN loads over the years examined (Janicki Environmental and Atkins, 2011). However, the wastewater treatment plant for the City of Belleair eliminated its surface discharge to the southern portion of Clearwater Harbor during the period of 2007 to 2008, just at the end of the timeline of loading estimates conducted for local waters (Rob Burnes, Pinellas County, personal communication).

As was noted in Tomasko et al. (2005) and elsewhere, Tampa Bay and Sarasota Bay show evidence of both substantial increases in TN loads over historical conditions, as well as significant reductions in TN loads over the past few decades. In Tampa Bay, TN loads are thought to have increased five-fold between 1938 and 1976, while Sarasota Bay's nitrogen loads were estimated to have increased by roughly the same amount (five-fold) from its undeveloped condition in the late 1800s up to 1988. Mostly due to upgrades to the processes involved in the treatment of domestic wastewater, annual TN loads to Tampa Bay

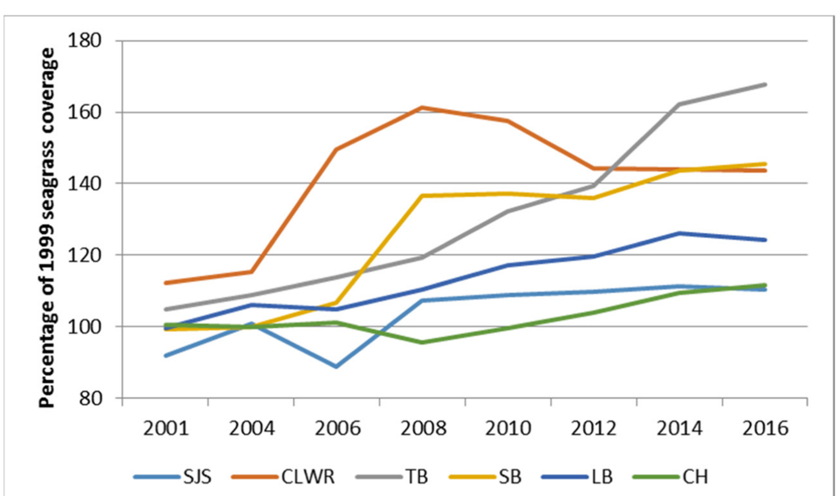

Fig. 4. Areal seagrass coverage per year, reported as a percentage of 1999 coverage. Data are from St. Joseph Sound (SJS), Clearwater Harbor (CLWR), Tampa Bay (TB), Sarasota Bay (SB), Lemon Bay (LB), and Charlotte Harbor (CH). Data from Southwest Florida Water Management District.

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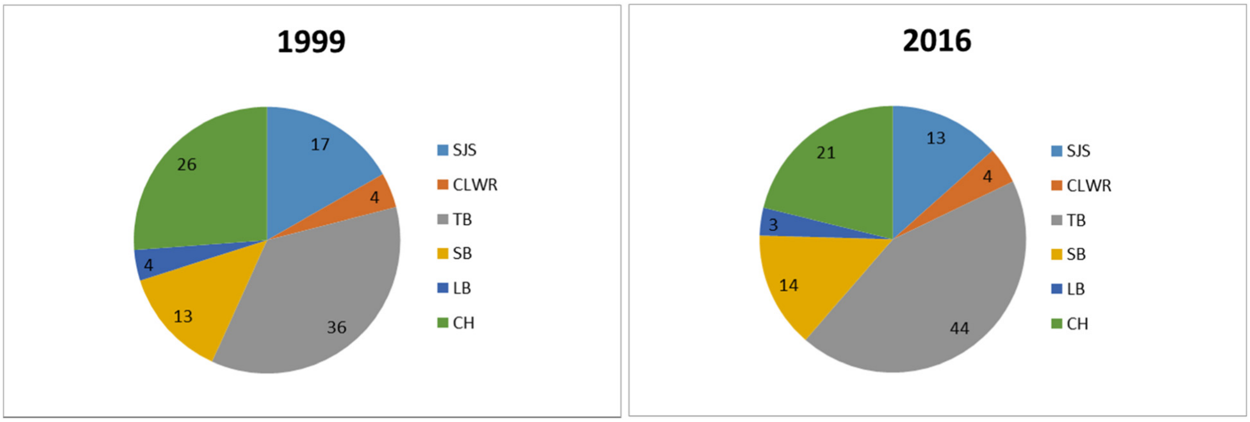

Fig. 5. Distribution of seagrass coverage in 1999 and 2016. Data are from St. Joseph Sound (SJS), Clearwater Harbor (CLWR), Tampa Bay (TB), Sarasota Bay (SB), Lemon Bay (LB), and Charlotte Harbor (CH). Data from Southwest Florida Water Management District.

declined by 57% between 1976 and the years 1992 to 1994. Despite ongoing population growth in the region, Tampa Bay's watershed-wide nutrient loads have not increased, when comparing the average of 1985 to 1992 against the average from 1993 to 2016. In Sarasota Bay, annual TN loads decreased by 64% in the two years between 1988 and 1990, as major wastewater treatment plant upgrades came on-line (PBS&J, 2009).

In Lemon Bay, nutrient loads were estimated to have increased by approximately 60% from reference conditions. A lower population size and the lack of any direct wastewater discharges to Lemon Bay have likely contributed to its relatively small increase in nitrogen loads from reference conditions, compared to Tampa and Sarasota Bays.

In Charlotte Harbor, the average annual TN load from the gaged Peace River was 1,632,932 kg TN $year^{-1}$ between 1985 and 1992. More than 20 years later, the 7 year period of 2009 to 2016 was estimated to have an average annual TN load of 1,657,427, a value < 2% different. These results suggest that while year to year variability might exist, the watershed-wide TN loads to Charlotte Harbor from the Peace River have not changed in any appreciable manner over the past three decades, a finding similar to that found for Tampa Bay.

4. Discussion

Recent reviews have painted a depressing portrait about trends in coverage of seagrass meadows worldwide (e.g., Orth et al., 2006; Waycott et al., 2009). These reviews give the impression that continued loss of seagrass is almost unavoidable, despite clear documentation of the causes of such losses (e.g., Larkum, 1976; Kemp et al., 1983; Orth and Moore, 1984; Cambridge and McComb, 1984; Silberstein et al., 1986; Bourcier, 1986; Reyes and Merino, 1991). However, there are a number of more recent examples in the literature that highlight the recovery of coastal ecosystems, when identified stressors have been adequately addressed. For example, Smith et al. (1981) not only documented the degradation of water quality and ecosystem health in Kaneohe Bay, Hawaii, they also identified the cause of the problem. In subsequent years, after domestic point source discharges to Kaneohe Bay were removed, the recovery of water quality and ecosystem health has been well documented (Hunter and Evans, 1995). A similar ecosystem response, including increased seagrass coverage, was also documented in the coastal waters of Adelaide, Australia, after the cessation of discharges from a domestic wastewater treatment plant (Bryars and Neverauskas, 2004). In a portion of the tidal Potomac River discharging to the Chesapeake Bay, Jones and Krauss (2009) documented the recovery of water quality and submerged aquatic vegetation following wastewater treatment facility upgrades.

In the stretch of Florida's southwest coast that corresponds with the estuaries considered in this paper, Florida Administrative Code (FAC) 403.086 dictates that wastewater discharges for the pollutants of

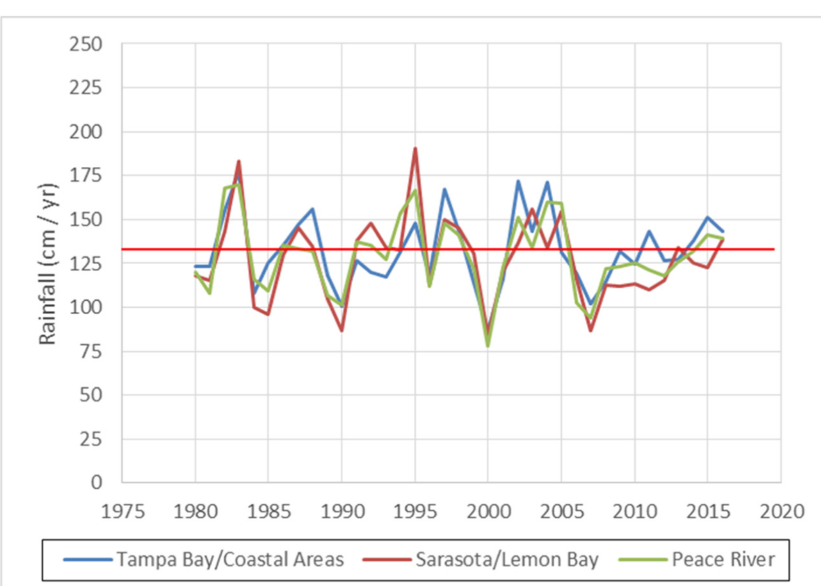

Fig. 6. Trends in rainfall (cm yr^{-1}) for the Tampa Bay/Coastal Areas, Sarasota/Lemon Bay and Peace River watersheds from 1980 to 2016. Red line represents average rainfall across the three watersheds from 1915 to 2016. Data from Southwest Florida Water Management District. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

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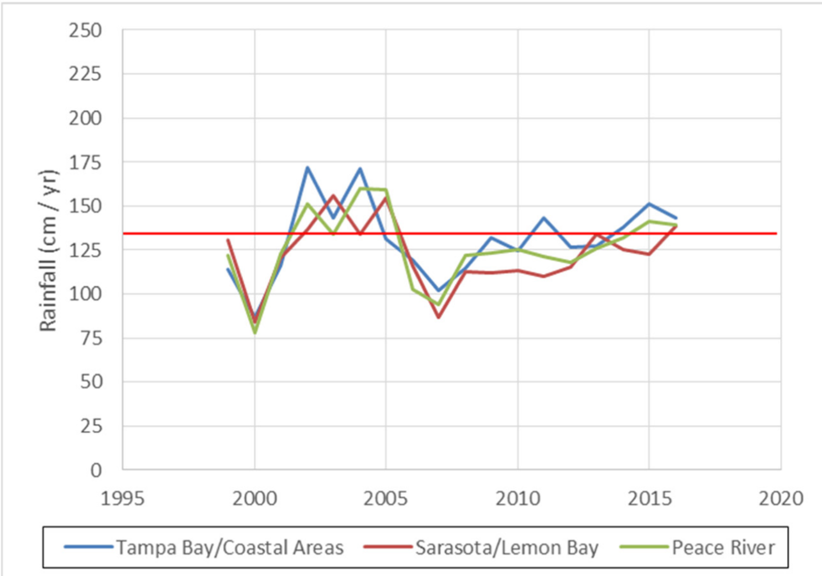

Fig. 7. Trends in rainfall (cm yr^{-1}) for the Tampa Bay/Coastal Areas, Sarasota/Lemon Bay and Peace River watersheds for the years 1999 to 2016. Red line represents average rainfall across the three watersheds over the period of 1915 to 2016. Data from Southwest Florida Water Management District. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 3
Estimated nitrogen loads by estuary for different time periods. Data for St. Joseph Sound and Clearwater Harbor are from Janicki Environmental and Atkins (2011). Data from Tampa Bay are from Pribble et al. (2001) and Sherwood et al. (2017). Data for Sarasota Bay are from PBS&J (2009). Data for Lemon Bay are from Tomasko et al. (2001). Data for Charlotte Harbor are from Squires et al. (1998) as well as the updated TN loading model for the Peace River's gaged watershed described above.

Estuary or watershed	Year(s)	Nitrogen load (kg TN $year^{-1}$)
St. Joseph Sound	1985 to 2008	78,925 to 332,937
Clearwater Harbor	1985 to 2008	49,895 to 222,260
Tampa Bay	1938	1,737,259
	1976	8,984,758
	1985–1992 average	3,569,993
	1993–2016 average	3,667,288
Sarasota Bay	1890	191,419
	1988	630,668
	1990	227,108
Lemon Bay	1850	81,345
	1995	129,713
Charlotte Harbor – Peace River	1985 to 1992 average	1,632,932
Charlotte Harbor – Peace River	2009 to 2015 average	1,657,427

Chemical-biological Oxygen Demand (CBOD), Total Suspended Solids (TSS), TN, and TP are not to exceed annual average concentrations of 5, 5, 3 and 1 mg/liter, respectively. This state legislation, known as the Grizzle-Figg Act, is geographically limited to that portion of the Gulf Coast of Florida that is the topic of this paper. In the 1980s, Florida also passed legislation that strictly controlled the discharge of stormwater pollutants from new development. While regulations differ regionally, in these watersheds the minimum amount of stormwater reduction, in terms of nitrogen loads, is between 30 and 40% for all new development (i.e., Harper and Baker, 2007). Existing development was not required to be retrofitted to meet the newer stormwater regulations, but 96 stormwater retrofit projects have been completed in the Tampa Bay watershed over the past 20 years, and 23 habitat restoration and/or stormwater retrofit projects have been completed in the Charlotte Harbor and Sarasota Bay watersheds over the past 20 years.

Not all of these six estuaries had previously been identified as having water quality problems related to human activity. For example, anthropogenic impacts to water quality and seagrass coverage have been well documented in Tampa Bay (e.g., Johansson, 1991, Johansson and Greening, 2000, Tomasko et al., 2005, Greening and Janicki, 2006, Greening et al., 2016, Sherwood et al., 2017) as well as in Sarasota Bay (e.g., Tomasko et al., 1996; Tomasko et al., 2005), Lemon Bay (Tomasko et al., 2001) and Clearwater Harbor (Janicki Environmental, Inc. and Atkins, 2011). However, seagrasses in Charlotte Harbor were not suggested to be particularly impacted by nutrient enrichment (Tomasko and Hall, 1999) in part because the major light attenuator in Charlotte Harbor is colored dissolved organic matter, rather than phytoplankton (McPherson and Miller, 1987). In St. Joseph Sound, there has been little evidence of a widespread impact to water quality via nutrient enrichment, although direct and indirect impacts to seagrass meadows associated with the construction of the Intracoastal Waterway have been documented (Janicki Environmental, Inc. and Atkins, 2011).

In a recent study, it was found that seagrass coverage in the Chesapeake Bay had increased by 17,000 ha between 1984 and 2015, a 23% improvement (Lefcheck et al., 2018). During the shorter time period of 1999 to 2016, the seagrass increase in these six Southwest Florida estuaries was 10,637 ha, an improvement of 38%. Before 1999, seagrass coverage had already increased by a combined 1534 ha in Tampa Bay and Sarasota Bay, compared to the 1980s. In total, seagrass coverage in these six estuaries had increased by 12,171 ha between the 1980s and 2016. The 12,171 ha increase is approximately 72% of the increase seen in the Chesapeake Bay, even though the Chesapeake Bay is approximately 7 times larger than the combined open waters of these six estuaries.

The patterns of seagrass recovery in the Chesapeake Bay (Lefcheck et al., 2018) and in these six estuaries in Southwest Florida are examples of large-scale ecosystem recovery that could guide management plans in other areas where seagrass losses have occurred. The basis for recovery and/or protection of seagrasses in both the Chesapeake Bay and in these six estuaries is readily apparent – a long term investment in nutrient management. In these waterbodies, improvements in water quality are noted as the main reason for seagrass recovery, and in all of the systems where seagrass recovery has occurred, the basis for water quality improvements has been reductions in sources of nutrient pollution (i.e., Johansson, 1991, Johansson and Greening, 2000, Tomasko et al., 2005, Greening and Janicki, 2006, Lefcheck et al., 2018),

As important as it is to reduce anthropogenic nutrient loads, the time lag between the initial (and typically the largest) reductions in nutrient loads and subsequent ecosystem responses can involve years. In Tampa Bay, a three-year time lag was found between upgrades to

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municipal wastewater treatment plants and the initial declines in chlorophyll-a and increases in water clarity. Additional time was needed for the initial increases in seagrass coverage in Tampa Bay to arise, in response to increasing water clarity (Johansson, 1991). In Sarasota Bay, the first evidence of substantial increases in seagrass coverage was obtained in 1994, several years after a 64% reduction in bay-wide nitrogen loads had been implemented. A similar pattern was noted in Gunston Cove, in the Chesapeake Bay watershed, where it took several years after an 80% reduction in point source nutrient loads was implemented until improvements in water clarity and increased coverage of submerged aquatic vegetation became evident (Jones and Krauss, 2009). Resource managers would be well-served by ensuring that the general public, regulators and permit-holders are fully aware of the need for patience, along with the message that success stories are out there.

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