

# The effects of Hurricane Irma on seagrass meadows in previously eutrophic estuaries in Southwest Florida (USA)

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## ABSTRACT

In six contiguous estuaries in Southwest Florida (USA) focused management actions over the past several decades have reduced watershed nutrient loads, resulting in an additional 11,672 ha of seagrass meadows between 1999 and 2016, an improvement of 32%. However, in September of 2017, Hurricane Irma made landfall in the state of Florida, affecting the open water and watersheds of each of these six estuaries. In response, seagrass coverage declined by 1203 ha between 2016 and 2018, a system-wide decrease of 3%. The range of decreases associated with Hurricane Irma varied from less than a 1% loss of seagrass coverage in St. Joseph Sound to declines of 7 and 11% in Clearwater Harbor and Lemon Bay, respectively. Areas with the largest losses between 2016 and 2018 were those systems where seagrass coverage had declined in prior years, indicating the effects of Hurricane Irma might have been intensified by prior impacts.

## 1. Introduction

In Southwest Florida (USA) it has long been established that the primary cause of historical losses of seagrass in local estuaries was increased nutrient loads from an expanding human population (i.e., Lewis et al., 1985; Lewis III, 1989; Haddad, 1989). In response, watershed-level management plans have been implemented that focused on reducing point source nutrient loads, while simultaneously seeking to reduce the impacts of continued population growth, mostly by focusing on stormwater retrofits. In Tampa Bay, this has brought about a 90% reduction in point source nitrogen loads, and an overall load reduction of ca. 60%, which has resulted in substantial reductions in both phytoplankton and macroalgae, with subsequent and sustained increases in seagrass coverage (e.g., Johansson, 1991; Johansson and Greening, 1999; Tomasko, 2002; Greening and Janicki, 2006; Greening et al., 2016; Sherwood et al., 2017; Beck et al., 2019). Prior studies on Sarasota Bay had shown that the biomass and productivity of seagrass meadows was inversely correlated with watershed-level nutrient loads (Tomasko et al., 1996) which supported ongoing efforts to reduce bay-wide nutrient loads. A similar recovery in seagrass coverage has been documented for Sarasota Bay, in response to similar reductions in point

and non-point source nutrient loads (Tomasko et al., 2005, 2018).

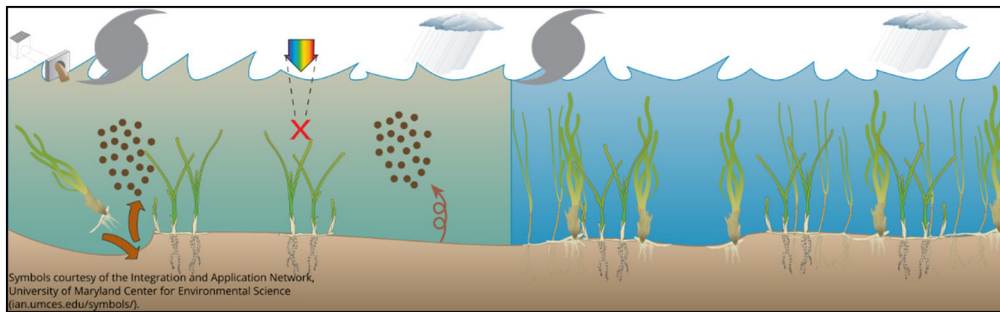
Between 1999 and 2016, seagrass coverage in the six contiguous estuaries of St. Joseph Sound, Clearwater Harbor, Tampa Bay, Sarasota Bay, Lemon Bay and Charlotte Harbor increased by 11,672 ha, a rise of 32% (Tomasko et al., 2018). The improvement in seagrass coverage between 1999 and 2016 ranged from an 11% increase in the relatively pristine waters of St. Joseph Sound to a 68% increase in the previously polluted waters of Tampa Bay (Tomasko et al., 2018).

In September of 2017, these six contiguous estuaries were then impacted by the passage of Hurricane Irma. Hurricane Irma was a Category 4 storm when it struck the Florida Keys, and remained a Category 4 storm when it first made landfall in the watershed of the southernmost of these six estuaries (Cangialosi et al., 2018). Hurricane Irma is the costliest storm to ever affect the state of Florida, in inflation adjusted dollars (National Hurricane Center, 2018). Irma remained a hurricane as it tracked south to north along Florida's west coast, and hurricane force winds and elevated rainfall impacted the watersheds of each of these six estuaries (Cangialosi et al., 2018).

The impacts of hurricanes on seagrass meadows have been previously studied by a number of researchers (e.g., Orth, 1976, Meyers et al., 2005, Byron and Heck, 2006, Steward et al., 2006, Anton et al.,

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**Fig. 1.** Graphical display of interaction between pollutant loads, water quality, seagrass health and the impacts of hurricanes on seagrass meadows. Symbols are courtesy of the Integration and Application Network, University of Maryland Center for Environmental Science. The left hand panel symbolizes conditions in degraded seagrass meadows, while the right hand panel symbolizes conditions in healthier meadows.

2009, Côté-Laurin et al., 2017, Hernández-Delgado et al., 2018). These studies indicate that impacts to seagrass meadows fall into two broad categories: 1) direct physical impacts of waves and currents, and 2) indirect impacts associated with elevated rainfall and impacts to water quality from increased pollutant loads. These two categories are not fully independent, as degraded water quality can potentially lessen the ability of seagrass meadows to withstand dislodgement via wave action, for example. Of particular importance in this paper, antecedent conditions would be expected to affect the resiliency of seagrass meadows, in terms of their ability to withstand direct and indirect impacts from hurricanes (Fig. 1).

In areas where pollutant loads have adversely impacted seagrass meadows through reduced water clarity, those meadows would be expected to have reduced density and biomass, as has been documented in Sarasota Bay (Tomasko et al., 1996). Those meadows might be more susceptible to seagrass losses due to erosion and subsequent resuspension of bottom sediments from increased wave action (Fig. 1, left side panel). In contrast, healthy seagrass meadows in areas with lower nutrient loads and better water quality might be less susceptible to direct and indirect impacts of hurricanes, as illustrated on the right side panel of Fig. 1.

This paper focuses on the impacts of the passage of Hurricane Irma on the seagrass resources of these six contiguous estuaries, which had, up until 2016, recorded impressive increases in seagrass coverage over the past few decades. The improved health of seagrass meadows in these six estuaries is expected to have enhanced their ability to withstand the impacts of the passage of Hurricane Irma, in 2017. By comparing estimates of seagrass coverage in the years just before and just after the passage of Hurricane Irma, this potentially enhanced resiliency was directly measured.

## 2. Materials and methods

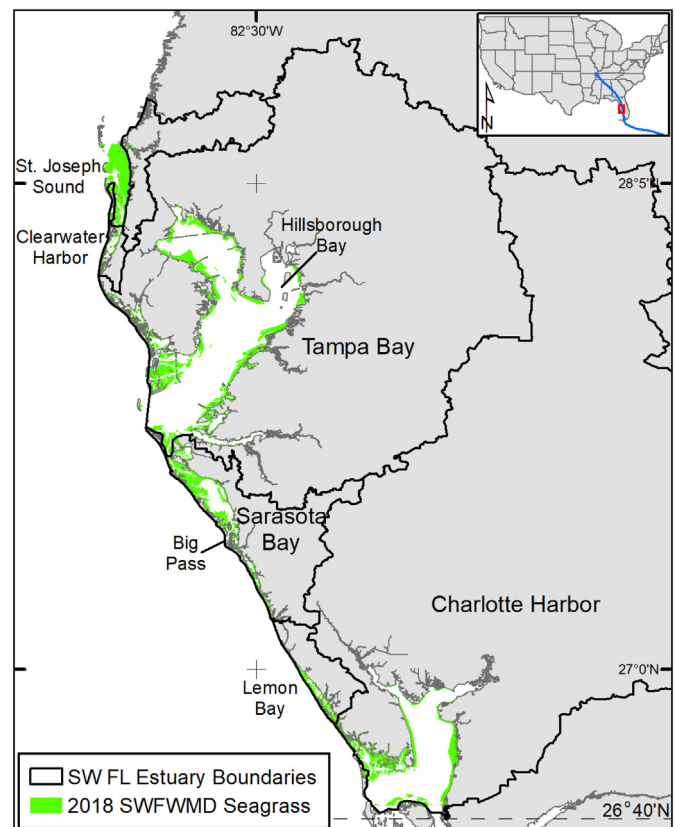
### 2.1. General description of locations

For this 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. 2). The region “Charlotte Harbor” includes only those areas north of 26°40' N latitude. As seen in the inset, Hurricane Irma passed through the study area (blue line denotes the path of the storm) in September 2017.

These subtropical systems experience warm, wet summers and mild, dry winters, with mean annual rainfall between 136 and 144 cm · year<sup>-1</sup>. More than half of the annual rainfall typically occurs during the typical June to September wet season (SWFWMD, 2018).

### 2.2. Seagrass mapping techniques

Since the late 1980s, estimates of seagrass coverage have been derived from photointerpretation of aerial photography acquired under strict protocols, as detailed in Tomasko et al. (2005). Additional information related to the usefulness of seagrass maps for any given year is contained within Tomasko et al. (2018). Based on assessments of



**Fig. 2.** Map showing southwest Florida watershed boundaries and 2018 seagrass coverage (Data Sources: US Geological Survey and Southwest Florida Water Management District; SWFWMD). Locations of Hillsborough Bay and Big Pass are noted. Inset shows study area in relationship to US, with blue line representing the path of Hurricane Irma in September 2017. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

water quality and pollutant loads, 1950 is considered to represent reference conditions for seagrass meadows, which were widely distributed throughout the region. In contrast, the 1980s represent degraded conditions, as pollutant loads were at or close to their highest levels in locations where such estimates are available, and water quality has been determined to have been much worse than in 1950 (i.e., Tomasko et al., 2005; Greening et al., 2016). For Charlotte Harbor and Lemon Bay, 1950 seagrass estimates are of limited value due to reduced water clarity in various locations on those dates when photography was collected. 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, 2018) and Sherwood et al. (2017). Starting in 2004, aerial photography and subsequent photointerpretation transitioned from scanned true color film media to digitally-acquired aerial imagery.

Seagrass coverage estimates are based on photography acquired during the winter dry season. These conditions generally allow for the acquisition of imagery more likely to be able to pick up the offshore, deeper margins of seagrass meadows. Seagrass maps are categorized based on the year during which photography was completed. For example, the latest seagrass maps, for the year 2018, are based on photography that was obtained after the passage of Hurricane Irma in September 2017, but prior to the outbreak of red tide events in Sarasota Bay and lower Tampa Bay, which had become widely established in the spring to summer of 2018 (Florida Fish and Wildlife Commission, 2018). In this example, seagrass maps for the year 2018 are likely influenced by climatic phenomena that occurred in 2017, but not the red tides that occurred later in 2018.

After the acquisition of aerial photography, field work is conducted to improve photointerpretation, with special attention focused on areas where the signature is not clear as to whether a signature represents seagrass, macroalgae, or a combination of the two. The coverage of more diminutive species of seagrass, such as those within the genus *Halophila*, are not captured through the use of aerial photography. Fortunately for this effort, species of *Halophila* are not commonly found in local waters, as documented in Tampa Bay (Tomasko et al., 2016; Sherwood et al., 2017).

### 2.3. Rainfall

The SWFWMD compiles rainfall data from more than 300 sites throughout its approximately 28,000 km<sup>2</sup> jurisdictional area, including the watersheds of all six of these estuaries. Data are available 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 adjacent watershed. 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 primary source of freshwater inflow to the estuary.

## 3. Results

### 3.1. Seagrass mapping

Table 1 contains results from seagrass mapping efforts for the six

**Table 1**

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 and other data from SWFWMD. Dash refers to no data for that location and time combination.

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	36,002
2001	4316	1345	10,555	3715	1046	7387	36,025
2004	4739	1383	10,938	3741	1113	7343	37,382
2006	4179	1792	11,452	3988	1098	7432	37,918
2008	5043	1934	11,998	5116	1158	7031	41,264
2010	5118	1887	13,313	5136	1229	7328	43,025
2012	5169	1727	14,019	5094	1256	7653	43,827
2014	5229	1724	16,307	5378	1323	8052	46,978
2016	5198	1721	16,857	5451	1304	8207	47,674
2018	5176	1606	16,451	5201	1168	7978	46,380

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 (Tomasko et al., 2005) and so the numbers from that estimate are not used here, as is also the case in Lemon Bay.

For St. Joseph Sound, seagrass coverage declined by 1487 ha between 1950 and 1999, a 24% decrease. Between 1999 and 2016, coverage increased by 495 ha, an 11% increase. Between 2016 and 2018, seagrass coverage declined by less than 1% in St. Joseph Sound.

In Clearwater Harbor, coverage decreased by 1235 ha between 1950 and 1999, a 51% decline. Between 1999 and 2016, coverage increased by 523 ha, a 44% improvement. Between 2016 and 2018, seagrass coverage declined by 7%. However, seagrass coverage in Clearwater Harbor peaked in 2008, with coverage in 2018 down 17% from peak values a decade earlier.

In Tampa Bay, seagrass coverage declined by 7596 ha between 1950 and 1982, a 46% decrease. Seagrass coverage then increased from 1982 to 1999 by 1292 ha, a 15% improvement. Between 1999 and 2016, coverage increased by 6804 ha, an improvement of 68%. Between 2016 and 2018, coverage decreased by 406 ha, a decline of 2%.

In Sarasota Bay, seagrass coverage declined by 641 ha between 1950 and 1988, a 15% decrease. Seagrass coverage then increased from 1988 to 1999 by 241 ha, a 7% improvement. Between 1999 and 2016, coverage increased by 1709 ha, an improvement of 46%. Between 2016 and 2018, coverage decreased by 250 ha, a decline of 5%.

In Lemon Bay, seagrass coverage declined by less than 1% between 1988 and 1999, well within the 2% error rate previously documented for seagrass mapping efforts in Southwest Florida (Tomasko et al., 2005). Seagrass coverage increased by 274 ha between 1999 and 2014, the year of peak coverage in Lemon Bay. Between 2014 and 2018, coverage declined by 155 ha, a 12% decrease, with most of that decline occurring between 2016 and 2018.

In Charlotte Harbor, seagrass coverage declined by less than 1% between 1982 and 1999, a rate of change well within the error rate associated with seagrass mapping efforts (Tomasko et al., 2005). Between 1999 and 2016, coverage increased by 852 ha, a 12% improvement. Between 2016 and 2018, coverage declined by 229 ha, a decrease of 3%.

For all six estuaries combined, coverage increased by 11,672 ha between 1999 and 2016, an improvement of 32%. During that time, the improvement in seagrass coverage was dominated by Tampa Bay, which accounted for 58% of the increase across the six estuaries (Fig. 3).

The dominance of Tampa Bay, in terms of seagrass increase between 1999 and 2016, is a function of several factors: 1) Tampa Bay is the largest estuary of the six, with an open water area more than twice as large as Charlotte Harbor, the second largest system (Tomasko et al., 2005), 2) Tampa Bay had the greatest percentage loss of seagrass coverage from historical conditions, resulting in more room for improvement than any of the other systems, and 3) the recovery in Tampa Bay, while substantial, was in-line with the substantial percent reduction in bay-wide nitrogen loads (Greening et al., 2016). The second largest source of system-wide increase (15%) came from Sarasota Bay, which is more than 80% smaller than Tampa Bay, which had more modest seagrass losses from historical conditions, but which also had a similarly impressive decrease in bay-wide nitrogen loads over the past few decades (Tomasko et al., 2018).

Between 2016 and 2018, system-wide seagrass losses of 1294 ha occurred, a decrease of 3%. The pattern of seagrass loss between 2016 and 2018 is illustrated in Fig. 4.

The results shown in Fig. 4 show that the pattern of system-wide seagrass losses between 2016 and 2018 differs from the increases between 1999 and 2016. For example, while Tampa Bay accounted for 58% of the total seagrass gains between 1999 and 2016, it only

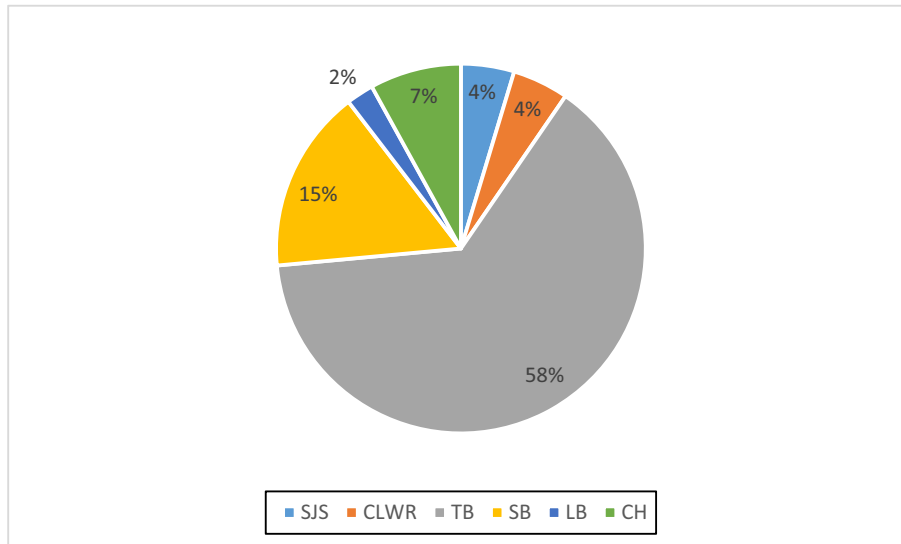


Fig. 3. Percentage of total increase in seagrass coverage, by individual bay, between 1999 and 2016. Data from SWFWMD.

accounted for 31% of the losses between 2016 and 2018. Thus, seagrass meadows in Tampa Bay decreased in response to Hurricane Irma at a rate lower than the rate of recovery during the prior 17 years. In contrast, while Clearwater Harbor accounted for just 4% of the seagrass gains between 1999 and 2016, it accounted for 9% of system-wide losses between 2016 and 2018.

In Clearwater Harbor, the 7% decline in seagrass coverage between 2016 and 2018 occurred in addition to prior losses, as seagrass coverage peaked in 2008. Between 2008 and 2018, seagrass coverage declined by 17% in Clearwater Harbor, a rate of loss greater than any of the five other estuaries. The locations of seagrass loss in Clearwater Harbor between peak coverage (2008) and the most recent estimates (2018) are shown in Fig. 5.

Lemon Bay accounted for just 2% of the total increase for all six systems between 1999 and 2016, but it accounted for 11% of the total seagrass loss between 2016 and 2018. In Lemon Bay, seagrass coverage peaked in 2014, and coverage in 2018 is 12% lower than 2014 estimates. The locations of seagrass loss in Lemon Bay between the year of peak coverage (2014) and the most recent mapping effort (2018) are shown in Fig. 6.

In Sarasota Bay, trends in seagrass coverage differ substantially between the northern portion of the bay, which is wider, with more pass influences and with a smaller watershed to open water ratio (Tomasko et al., 1992) than in the southern portion of the bay, which is narrower, with lower flushing rates (Sheng and Peene, 1992) and a higher watershed to open water ratio (Tomasko et al., 1992). In the northern part of the bay, seagrass coverage has increased by more than 60% over the past 20 years, while in the southern part of the bay, coverage is lower now than it was in the late 1980s (Fig. 7).

### 3.2. Rainfall

Between 1996 and 2018, there is no monotonic trend in rainfall in any of the watersheds considered here, although periods of elevated rainfall are evident (Fig. 8).

The years 1997 and 1998 were associated with elevated rainfall, mostly due to the 1997 to 1998 El Niño event. This was followed by reduced rainfall in the years 1999 and 2000, which were the first two years of the system-wide coordinated seagrass mapping efforts in Southwest Florida. Increased rainfall was then recorded for the years

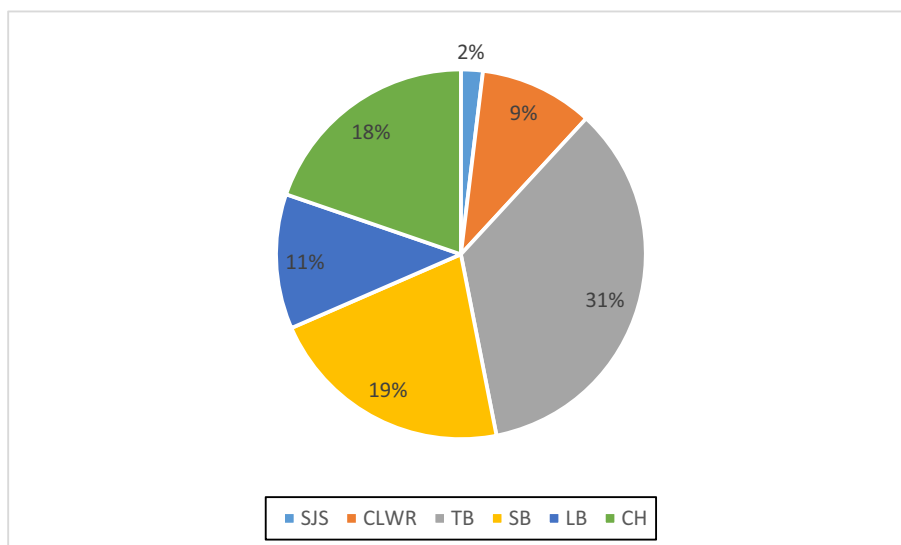


Fig. 4. Percentage of total seagrass decline between 2016 and 2018, by individual bay. Data from SWFWMD.



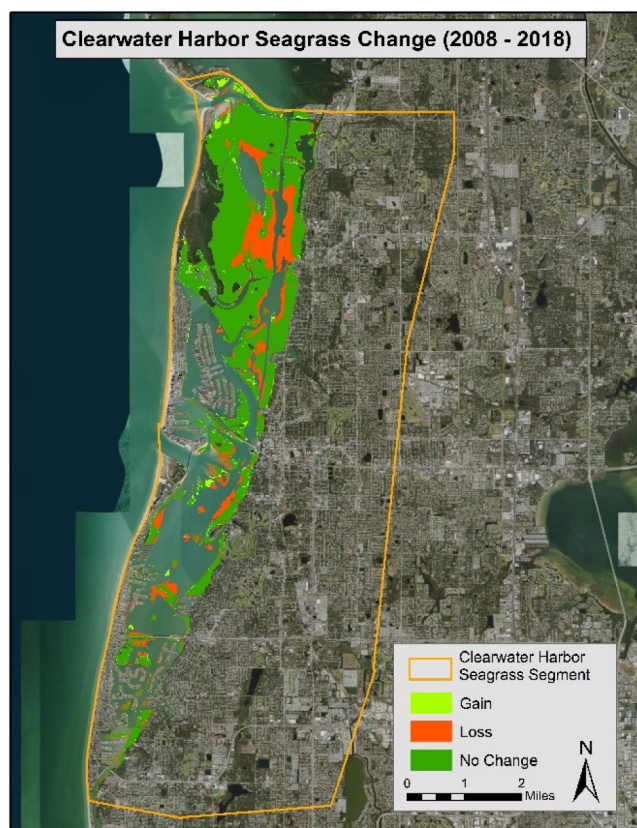


Fig. 5. Pattern of seagrass coverage that was stable, areas of gain, and areas of loss between 2008 and 2018 in Clearwater Harbor.

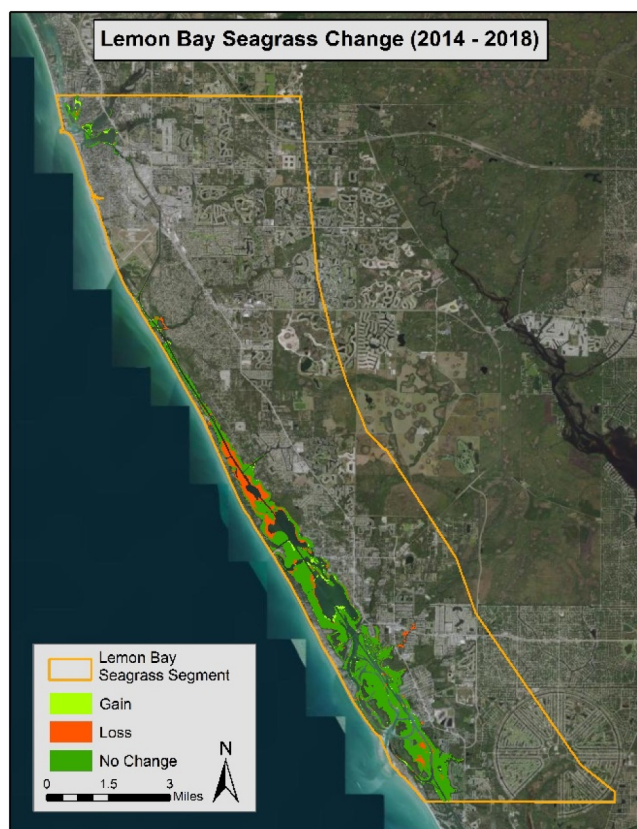


Fig. 6. Pattern of seagrass coverage that was stable, areas of gain, and areas of loss between 2014 and 2018 in Lemon Bay.

2003 to 2005, which included the busy hurricane seasons of 2004 and 2005, when at least one of each of the three watersheds was affected by rainfall from Hurricanes Charley, Frances, and Jean, in 2004, or Wilma, in 2005. Rainfall declined during the years 2006 to 2009, followed by a general pattern of increase between 2010 and 2018.

The variation from the long-term average for each watershed for the years 1996 to 2018 is shown in Fig. 9.

The rainfall data in Fig. 9 show a pattern wherein the three watersheds display similar rainfall patterns over time. The elevated rainfall amounts in 2003 to 2005 are similar to the amount of surplus rainfall during the 1997 to 1998 El Niño event. And while the years of 2007 to 2018 show a pattern of a general increase in rainfall, the trend is back towards the long-term average, rather than a trend resulting in exceptionally wet years. Across the three watersheds, the amount of rainfall in 2017, which included the passage of Hurricane Irma, was lower than the annual amount of rainfall that occurred in the 1997 to 1998 El Niño event, as well as the rainfall amounts seen in the 2004 and 2005 hurricane seasons.

#### 4. Discussion

As was described in Tomasko et al. (2018) the six contiguous estuaries considered in this paper are all covered by wastewater treatment plant guidance contained in Florida Administrative Code 403.086, which dictates that wastewater discharges for the pollutants of Chemical-biological Oxygen Demand, Total Suspended Solids, Total Nitrogen, and Total Phosphorus are not to exceed annual average concentrations of 5, 5, 3 and 1  $\text{mg} \cdot \text{L}^{-1}$ , 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 addition to the required upgrades to wastewater treatment plants, the state of Florida passed legislation in the 1980s that requires the discharge of stormwater pollutants from new development to be routed through stormwater treatment systems that are designed to reduce pollutant concentrations and loads. In response, the six contiguous estuaries that are the focus of this paper all show a pattern of reduced pollutant loads, increased water quality, and an overall pattern of seagrass increase between the 1980s and 2016 (i.e., Tomasko et al., 2018, and references therein).

During the period of 1999 to 2016, seagrass coverage in these six estuaries increased by 11,672 ha, an improvement of 32% (Tomasko et al., 2018, and Table 1). The species composition of seagrass meadows in these six systems appears to have changed somewhat over the years. The portion of St. Joseph Sound with the most persistent meadows over time are those which are dominated by turtle grass (*Thalassia testudinum*) while deeper areas where gains had occurred are dominated by manatee grass (*Syringodium filiforme*) and shoal grass (*Halodule wrightii*; Janicki Environmental Inc. and Atkins, 2011). In Tampa Bay, a similar pattern has arisen, the seagrass meadows that have been stable over the years are mostly dominated by *T. testudinum*, while much of the recent increased coverage is associated with the species *S. filiforme* and *H. wrightii* (Sherwood et al., 2017).

This substantial and widespread increase in seagrass coverage is in contrast to trends in the Indian River Lagoon (e.g., Lapointe et al., 2020) and Biscayne Bay (Lirman et al., 2016) where widespread losses of seagrass coverage have been linked to inadequate water quality. In both the Indian River Lagoon and Biscayne Bay, it appears that macroalgae have been an important mechanism of seagrass impacts, above and beyond impacts from phytoplankton alone (Lirman et al., 2016; Lapointe et al., 2020).

However, the six estuaries considered here were then impacted to varying degrees by the passage of Hurricane Irma, in September 2017 (Cangialosi et al., 2018). Hurricane Irma was the costliest hurricane (in inflation-adjusted dollars) to have ever made landfall in the state of Florida (National Hurricane Center, 2018). Considering the amounts of funding spent on wastewater and stormwater projects, along with

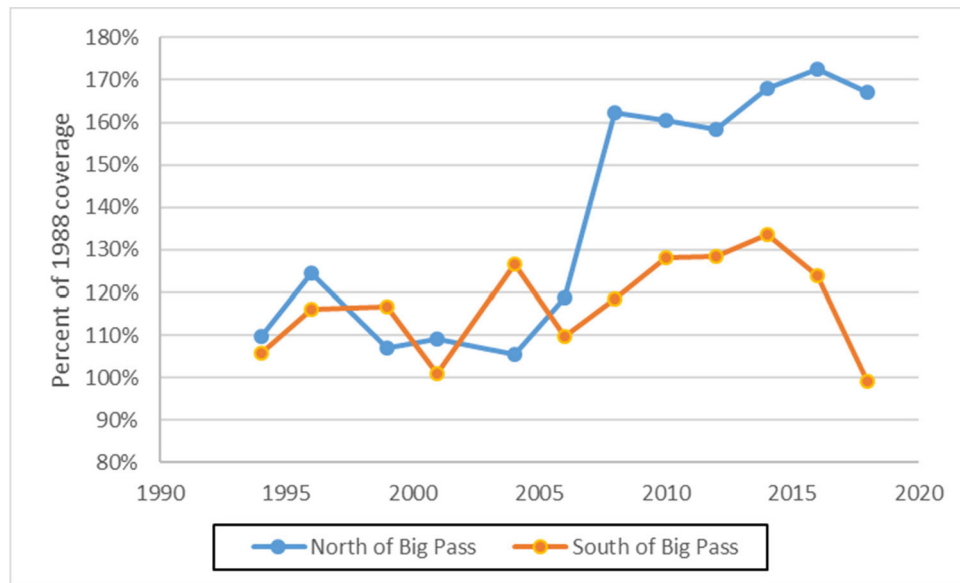


Fig. 7. Trends in seagrass coverage (ha) between northern and southern portions of Sarasota Bay.

numerous coastal restoration efforts, the concern among resource managers was that the seagrass recovery brought about in these six estuaries could have been seriously set back by impacts from Hurricane Irma.

Prior literature shows that seagrass responses to hurricanes and other tropical events can vary substantially. In 2004, Hurricane Charley had only minor and localized impacts on the seagrass meadows of Charlotte Harbor (Meyers et al., 2005; Carlson et al., 2010). In response to the busy 2004 hurricane season, the seagrass resources of Florida's Indian River Lagoon exhibited only minor and localized impacts as well (Steward et al., 2006). In coastal Alabama, Byron and Heck (2006) recorded only minor impacts to seagrass meadows from Hurricanes Ivan and Katrina, in 2004 and 2005, respectively. Similarly, Anton et al. (2009) reported minor impacts to seagrass in the northern Gulf of Mexico after the 2005 passage of Hurricane Katrina.

In contrast, extensive damage to seagrass meadows was found offshore of Puerto Rico's Culebra Island, after the area was impacted by the dual hurricanes of Irma and Maria, in 2017 (Hernández-Delgado

et al., 2018). In Madagascar, seagrass meadows were substantially impacted by 2013's Cyclone Haruna (Côté-Laurin et al., 2017). And in the Chesapeake Bay, the heavy rains and massive influx of freshwater, sediments and nutrients associated with 1972's Hurricane Agnes resulted in widespread impacts to seagrasses, including the almost complete loss of the species *Zostera marina* in most of the bay (Orth, 1976).

The fact that Hurricane Irma had relatively minor impacts on seagrass coverage across the six continuous estuaries, where overall meadows declined by just 3%, does not mean that impacts did not occur on a local scale. And while the Chesapeake Bay's seagrass resources were decimated by inflows of freshwater and pollutants from 1972's Hurricane Agnes (Orth, 1976), Hurricane Irma was not associated with unprecedented rainfall across the region. Instead, the rainfall amounts across the region in 2017 were less than 20 cm above the long-term average. Across these six estuaries, greater watershed-level rainfall amounts were recorded during the years associated with the 1997 to 1998 El Niño, as well as the busy hurricane seasons of 2004 and 2005 (Fig. 9). Comparing the mapping efforts before (1996) and after (1999)

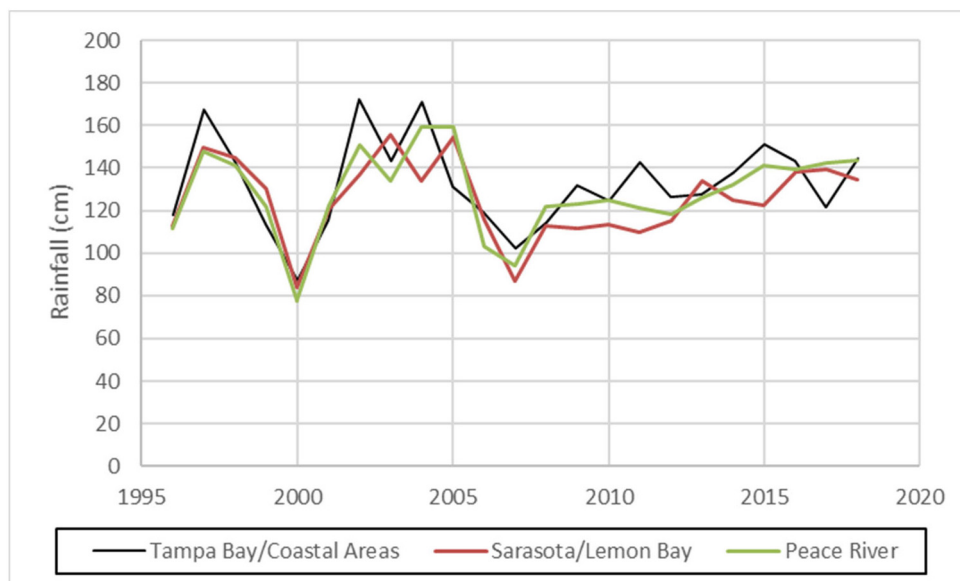
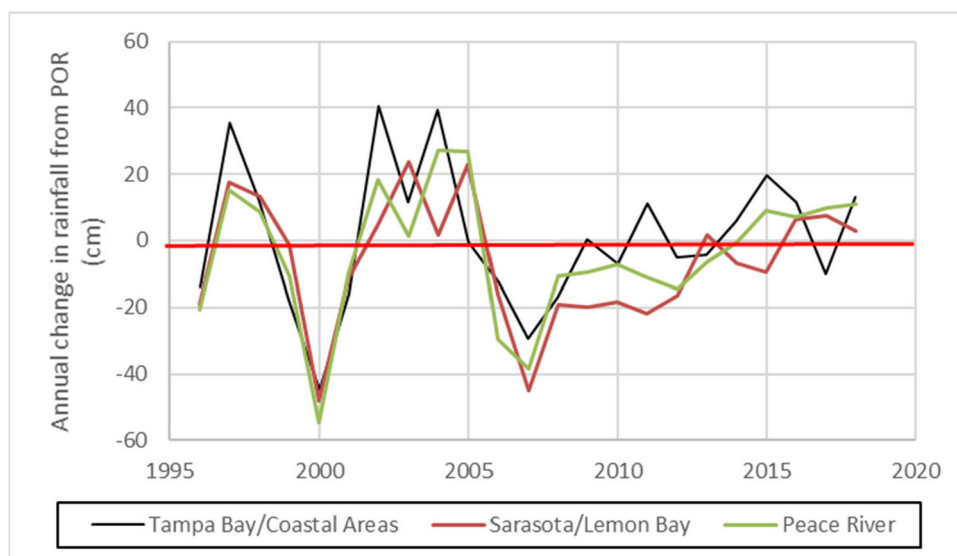


Fig. 8. Trends in rainfall ( $\text{cm} \cdot \text{yr}^{-1}$ ) for the Tampa Bay/Coastal Areas, Sarasota/Lemon Bay and Peace River watersheds from 1996 to 2018. Data from SWFWMD.



**Fig. 9.** Annual change in rainfall (cm) from period of record (1915 to 2018) average for the years 1996 to 2018. Data shown are compared to period of record averages individually calculated for the Tampa Bay/Coastal Areas, Sarasota/Lemon Bay and Peace River watersheds. Data from SWFWMD.

the 1997 to 1998 El Niño event, seagrass coverage in Tampa Bay and Charlotte Harbor declined by 8 and 6%, respectively, indicating impacts greater than those seen in response to Hurricane Irma in those same systems. In contrast, Lemon Bay's seagrass coverage declined by less than 1% between 1996 and 1999, indicating Hurricane Irma was more damaging to Lemon Bay's seagrass resources than the 1997 to 1998 El Niño event.

Although the six contiguous estuaries as a whole are still ahead of where they were in the 1980s and 1990s, in terms of seagrass coverage, not every part of every system appears to be equally healthy, using this metric. In Clearwater Harbor, seagrass coverage peaked in 2008. Since then, seagrass meadows in Clearwater Harbor have declined by 17%, with most of the loss between 2008 and 2018 occurring in those meadows that were farthest offshore from both the mainland and the barrier island. These waters are typically the deepest portions of the system, and losses in those areas suggest that water clarity might have declined enough to reduce seagrass coverage by impacting the farthest offshore, deepest growing seagrass meadows.

In Lemon Bay, seagrass coverage started to decline in 2014, prior to Hurricane Irma. Since 2014, seagrass meadows are down by 12% in Lemon Bay, although they remain 11% higher than they were in 1999. In Lemon Bay, the predominant area of seagrass loss is in the far northern part of the bay, in an area roughly equidistant from the two closest flushing inlets, Venice Inlet to the north and Stump Pass to the south. Losses of seagrass in Lemon Bay appear to have been concurrent with increased abundance of macroalgae in mostly shallower waters than the areas where seagrass loss occurred in Clearwater Harbor (Tomasko, personal observation). Macroalgae have also been posited as a mechanism through which nutrient enrichment has degraded seagrass meadows in the Indian River Lagoon (Lapointe et al., 2020).

In those systems with relatively minor decreases in seagrass between 2016 and 2018, not all portions of those bays responded to Hurricane Irma in an equal fashion. In Tampa Bay, although bay-wide coverage only decreased by 2% between 2016 and 2018, the most heavily impacted part of Tampa Bay, Hillsborough Bay, had percentage declines in seagrass coverage ten-times the bay-wide average. However, Hillsborough Bay still has more seagrass than was mapped in the 1980s and 1990s.

In Sarasota Bay, the pattern of seagrass recovery varied substantially in different parts of the bay. In the area north of Big Pass, seagrass coverage was 67% higher in 2018 compared to 1988. In contrast, lower portions of Sarasota Bay showed less than a 1% increase

over that same 30-year period. The lack of improvement in the southern part of Sarasota Bay is related to two phenomena: 1) an approximate 30% increase in seagrass coverage between 2001 and 2014, and 2) starting in 2014, a subsequent loss of seagrass coverage approximately equal to the preceding increase. The recent deterioration of seagrass coverage in the lower portion of Sarasota Bay cannot be blamed on Hurricane Irma alone, as losses preceded 2017. In those waters, macroalgae are a noted, but insufficiently quantified, pathway through which nutrient enrichment is potentially impacting seagrass meadows (Lapointe personal observation). In the lower portions of Sarasota Bay, it appears that recent increases in anthropogenic sources of pollution need to be addressed to reverse recent seagrass loss (Tomasko and Keenan, 2019).

The implications of our findings, related to conservation and management of seagrass meadows, is that actions that improve water quality may help to increase the resiliency of seagrass meadows to storm events. Seagrass losses after the passage of Hurricane Irma were not evenly distributed across the six systems, or within the six systems. For example, losses in Tampa Bay were fairly minor, but most of the losses were in Hillsborough Bay, the portion of the bay with the worst water quality. In Sarasota Bay, seagrass losses associated with Hurricane Irma were mostly in those parts of the bay that had exhibited a pattern of loss prior to the hurricane. Losses of coverage in the two systems with the largest proportional declines, relative to prior improvements, were in Clearwater Harbor and Lemon Bay, two waterbodies that had shown evidence of prior declines. In contrast, those waterbodies, or portions of waterbodies, with a sustained history of stable or increasing seagrass coverage, such as St. Joseph Sound, lower portions of Tampa Bay, and upper Sarasota Bay mostly had minor losses, if any, after the passage of Hurricane Irma.

In these local waters, it has been established that sustained efforts to reduce point and non-point source nutrient loads have allowed for substantial improvements in both water quality and seagrass coverage. The findings contained in this paper suggest that these efforts have likely increased the ability of these seagrass meadows to withstand the direct and indirect impacts of hurricanes, as well.

#### CRediT authorship contribution statement

**D. Tomasko:** Conceptualization, Formal analysis, Methodology, Validation, Writing - original draft. **M. Alderson:** Data curation, Formal analysis, Funding acquisition, Project administration, Writing - review



& editing. **R. Burnes:** Data curation, Formal analysis, Funding acquisition, Project administration, Writing - review & editing. **J. Hecker:** Data curation, Formal analysis, Funding acquisition, Project administration, Writing - review & editing. **N. Iadevaia:** Data curation, Formal analysis, Funding acquisition, Project administration, Writing - review & editing. **J. Leverone:** Data curation, Formal analysis, Funding acquisition, Project administration, Writing - review & editing. **G. Raulerson:** Data curation, Formal analysis, Funding acquisition, Project administration, Writing - review & editing. **E. Sherwood:** Data curation, Formal analysis, Funding acquisition, Project administration, Writing - review & editing.

### Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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