Insights from 15 years of benthic infaunal monitoring in a coastal lagoon system

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Abstract Benthic infaunal communities are important indicators of environmental change because they are comprised of organisms with limited mobility that respond rapidly to stress. As part of the Comprehensive Everglades Restoration Plan to restore natural water flows across the Florida peninsula, infaunal communities have been monitored since 2005 in relation to changing water quality and sediment characteristics at 9 sites in the southern Indian River Lagoon (IRL) and St. Lucie Estuary (SLE). Abiotic and biological differences separated the sites into 3 zones, with salinity and the abundance of fine-grained sediments emerging as major drivers of infaunal abundance, species richness and distribution. Degraded communities in the middle SLE were populated by opportunistic and pollution-tolerant taxa, while communities in the southern IRL were abundant and biodiverse. A total of 76 taxa and one-third of all infauna were lost across the three zones in 2016 and 2017, which was likely caused by harmful algal blooms and discharges of sediment and nutrient-laden inland freshwater following an El Niño event and Hurricane Irma. This study highlights the importance of long-term monitoring to inform adaptive management practices and lays the groundwork for further analyses to understand how natural and anthropogenic stressors affect this dynamic system.

Keywords benthos, Florida, Indian River Lagoon, indicator species, infauna, St. Lucie Estuary

Introduction

Benthic infauna are found in the soft sediments of aquatic ecosystems where they play crucial roles in maintaining healthy environments. These small burrowing organisms, including polychaetes, bivalves and other macroinvertebrates, form communities that consume settled and suspended organic matter (Word 1978, Tenore et al. 2006), aerate and cycle nutrients in sediments (Rysgaard et al. 1995, Mermillod-Blondin et al. 2004) and serve as prey for higher level organisms (Virnstein 1977, Seitz et al. 2001). Benthic infauna are also excellent indicators of habitat quality because they remain stationary and respond rapidly to stressors at levels that are often undetected by larger animals. As such, infauna are monitored worldwide as benchmarks of environmental change and have been studied for decades in estuaries throughout Florida (e.g. Bloom et al. 1972, Lewis 1984, Mason et al. 1994, McRae and Madley 2001, Walton et al. 2013).

The Indian River Lagoon (IRL) estuary occupies approximately one-third of Florida's east coast, spanning from temperate to subtropical climate zones and supporting highly biodiverse ecosystems that are critical to the environmental and

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economic health of the region. The southern IRL connects with the St. Lucie Estuary (SLE) to the west and with the Atlantic Ocean through the St. Lucie Inlet to the east. This system is at the eastern edge of the Everglades watershed that historically delivered freshwater originating from the Kissimmee River south across the peninsula and toward Florida Bay (LoSchiavo et al. 2013). Propelled by rapid population growth and development, watershed hydrology was altered in the mid-1900s to drain lands, provide flood protection and store water for residential and agricultural uses (Light and Dineen 1994). Among these alterations was the connection of the SLE to a network of drainage canals that diverted freshwater from central Florida east toward the IRL and Atlantic Ocean. This destabilized salinity regimes and delivered excess nutrients, suspended sediments and other pollutants to the SLE and southern IRL that degraded habitats and threatened biodiversity (Sime 2005, Wilson et al. 2005, Lapointe et al. 2017).

In 2000, the Comprehensive Everglades Restoration Plan (CERP) was launched by the State of Florida and the U.S. Federal Government to restore the natural hydrology of the Everglades watershed while protecting developed lands and resources needed by a continually growing human population (RECOVER 2019). CERP employs an adaptive management approach that relies on monitoring data to guide restoration activities. As part of this program, benthic infauna and key environmental parameters have been monitored quarterly in the southern IRL and SLE since 2005. The purpose of this paper is to present overall trends from a wealth of accrued data, serving as a springboard for more detailed analyses designed to provide a clear picture of ecosystem processes that will further inform management actions in this unique estuary system.

Materials and Methods

Field Procedures. Benthic infaunal sampling was performed quarterly at 9 fixed sites (mean depth 2.14 ± 0.02 m, Figure 1, Table 1) in the southern IRL and SLE from February 2005 through October 2019. Replicate sediment samples (n = 3) were collected for infaunal analyses with a petite Ponar grab (225-cm^2 sample area) deployed from a 21-ft Carolina Skiff. After sieving (500 μm) to isolate taxa, the samples were immediately preserved in a solution of $4 - 7\%$ buffered formalin with rose bengal stain (Rumohr 2009). Three additional grabs were collected periodically to estimate the mean volume of sediment per sample prior to sieving, which varied across sites based on sediment type (Table 1) and degree of compaction. During each sampling event, bottom salinity (ppt), dissolved oxygen (mg L^{-1}), and pH were measured with a YSI ProPlus multiparameter meter (YSI Inc., Yellow Springs, OH). Turbidity (NTU) was measured with a Hach 2100P turbidimeter (Hach Co., Loveland, CO). Annually since April 2009, an Ogeechee corer was used to collect one 5-cm depth core per site for granulometric analysis. Core samples were placed on ice and stored at -20°C upon return to the laboratory.

Laboratory Procedures. After $2 - 4$ weeks of fixation, infaunal samples were re-sieved (500 μm) and transferred to 70% ethanol. Using stereomicroscopy (6x magnification), organisms were isolated from residual sediment, enumerated and identified to the lowest possible taxonomic level. Sorted samples were transferred to new 70% ethanol for archival storage.

Sediment cores for granulometric analysis were thawed at room temperature and placed in pre-weighed aluminum dishes. After weighing to the nearest 0.01 g, the samples were dried at 100°C for 24 h, cooled and re-weighed. Samples were mixed for 10 min in a solution of 25% sodium hexametaphosphate in tap water, which disaggregates sediment particles and aids in sieving (Bamber 1982). Mixed samples were left overnight at room temperature, rinsed and sieved (63 μm) to discard the

Figure 1. Nine long-term benthic infaunal and environmental monitoring sites in the southern Indian River Lagoon and the St. Lucie Estuary.

Table 1. Descriptions of the 9 long-term benthic infaunal and environmental monitoring sites in the southern Indian River Lagoon and the St. Lucie Estuary.

	Latitude	Longitude	Meters to Shore	Site Description and Nearby Attributes[1]	Sediment Description[2]
M1	27.32475	-80.33227	18	Vegetated natural shore at Savannas Preserve State Park; 100 m SE of Prima Vista Bridge	Fine to muddy sand, shell hash, large organic debris; medium sorted; soft to medium stiff
M2	27.27103	-80.32198	12	Vegetated natural shore with boardwalk added in 2020; 100 m S of Kellstadt Bridge, 2.1 km N of C-24 canal	Muddy sand, shell hash, large organic debris; medium sorted; soft to medium stiff
M3	27.22857	-80.28807	380	Residential shore; 180 m to OR, 490 m to SWO, 500 m SW of Britt Creek, 2.7 km N of C-23 canal	Mud to muddy sand, occasional mixture of shells; well sorted to unsorted; very soft
M4	27.18233	-80.26545	318	Residential and commercial shore; 320 m to SWO, 340 m to OR, 800 m NE of Danforth Creek, 1 km N of Palm City Bridge	Mud; well sorted to unsorted; very soft
M5	27.20420	-80.25000	530	Commercial shore; 260 m to OR, 800 m W of Roosevelt Bridge, 1.8 km W of Krueger Creek	Mud to muddy sand, occasional mixture of shells; well sorted to unsorted; very soft
M6	27.21340	-80.21563	520	Residential shore; 400 m to OR, 1.2 km to SWO, 1.3 km SE of Warner Creek, 1.8 km NW of Evans Crary Bridge	Muddy sand, shell hash; medium sorted; very soft to medium stiff
M7	27.17290	-80.19773	275	Residential shore; 300 m NW of Willoughby Creek, 345 m to SB, 1.5 km W of Indian River Lagoon at St. Lucie Inlet	Fine sand, occasional muddy deposits; medium to well sorted; medium stiff
M9	27.19963	-80.17443	580	Vegetated residential shore; 250 m to SB, 820 m to SWO, 1.6 km S of Ernest Lyons Bridge, 4 km N of St. Lucie Inlet	Fine sand, occasional muddy deposits and mixture of shells; medium sorted; medium stiff
M11	27.39867	-80.28242	810	Vegetated natural shore E of Savannas Preserve State Park; on edge of SB, 8 km S of Ft. Pierce Inlet	Fine sand, occasional muddy deposits and mixture of shells; medium sorted; medium stiff

[1] Distances to oyster reefs (OR) and seagrass beds (SB) based on data layers available at geodata.myfwc.com/datasets. Distances to canals and stormwater outfalls (SWO) based on data from the South Florida Water Management District and the Martin County Public Works Department.
[2] Descriptions from visual and tactile field assessments following scales and terminology from Wentworth (1922) and Folk et al. (1970).

finest grains that harden in the oven, and dried again for 24 h at 100°C. Dried samples were cooled, weighed and sorted for 10 min with a series of geological sieves (4 mm, 2 mm, 500 μm, 250 μm, 125 μm and 63 μm) in a Meinzer II sieve shaker (CSC Scientific Inc., Fairfax, VA). The weight of the sediment retained by each sieve was recorded, and the weight of the <63 μm fraction was calculated by subtracting the total weight of the sieved sediment from the dry weight of the sample prior to adding the sodium hexametaphosphate solution. Fraction weights were converted to percent dry weights per sample.

Data Analysis. Univariate statistical analyses were conducted in The Real Statistics add-in package for Microsoft Excel (real-statistics.com). Following Levene's tests that revealed all abiotic environmental data were heteroscedastic, Welch's analyses of variance (ANOVA, $\alpha = 0.05$) and Games-Howell post-hoc tests were used to detect differences among sites for each parameter. Similarity percentage (SIMPER) analyses were conducted with the PRIMER v5 multivariate statistics software package (Clarke and Warwick 2001) to determine the key taxa responsible for characterizing communities at each site throughout the 15-year period. A key taxon was defined as the top contributor to within-site similarity among replicate samples during each sampling event. Prior to analysis, infaunal count data were normalized by volume and square root transformed.

Results

Across all sites, a total of 1,560 infaunal samples were collected, 339,983 individuals were enumerated and 440 taxa from 16 phyla were identified. Per sample infaunal richness and density ranged from 0 to 68 taxa and 0 to 17,914 individuals L^{-1}, respectively.

Spatial Variation. Key abiotic and infaunal characteristics varied considerably across the 9 monitoring sites (Table 2). As expected, mean bottom salinity was lowest at M1 farthest up the St. Lucie River and increased moving toward M7 at the entrance to the IRL ($p < 0.001$). Pairwise comparisons with the more ocean-influenced M7 to M11 revealed that SLE sites exhibited lower dissolved oxygen (M2 and M3, $p \leq 0.039$), lower pH (M1 to M4, $p \leq 0.010$) and higher turbidity (M1 and M4, $p \leq 0.025$). Sites M3 to M5, where the north and south forks of the St. Lucie River converge, were characterized by the greatest percentage of fine-grained sediments <63 μm ($p \leq 0.002$) of all 9 sites and languishing infaunal communities (i.e. lowest total individuals, total taxa and unique taxa). In contrast, infaunal communities at M7 and M9 near the St. Lucie Inlet contained the most individuals, total taxa and unique taxa. Annelids were the most abundant infauna overall (Table 2) but were largely displaced by bivalves at M2 to M4. The relative percentage of ostracods was highest at the oligohaline M1 and the euhaline M11. Further observations indicated that different species comprised these two populations. Reaching 55% per sample, insect larvae (mainly midges, Family Chironomidae) were the primary contributors of the 'Other' category at M1.

A closer investigation via SIMPER analysis revealed 42 key taxa responsible for driving community composition at the 9 sites (Table 3). These included 9 core taxa found at all sites throughout the 15-year period: the annelids *Mediomastus californiensis*, *Paraprionospio pinnata*, *Spiochaetopterus* sp. and *Streblospio* sp.; the amphipods *Ampelisca abdita* and *Grandidierella bonnieroides*; the bivalves *Mulinia lateralis* and *Tellina* sp.; and the gastropod *Acteocina canaliculata*. Most of the 42 taxa were either well distributed among the sites or more abundant in the IRL. However, a few taxa were better represented in the SLE: the annelid *Laeonereis* sp.; the amphipod *Apocorophium* sp.; the bivalves *Mytilopsis*

Table 2. Key abiotic and infaunal characteristics of all 9 sites based on quarterly data from 2005 – 2019. Mean % sediments <63μm are based on annual April measurements since 2009. All means are ± 1 SE.

	Mean Bottom Salinity (ppt)	Mean Bottom Oxygen (mg/L)	Mean Bottom pH	Mean Surface Turbidity (NTU)	Mean Sediment <63 μm (% dry wt.)	Total Infauna	Total Taxa	Unique Taxa	Annelida	Amphipoda	Ostracoda	Bivalvia	Gastropoda	Other
											(% relative abundance)			
M1	1.5 ± 0.3	5.9 ± 0.3	7.8 ± 0.0	7.7 ± 0.4	2.3 ± 0.3	38,254	102	9	40.1	4.9	24.3	2.2	10.0	18.5
M2	6.5 ± 0.9	5.2 ± 0.2	7.7 ± 0.0	5.9 ± 0.4	5.0 ± 0.5	40,615	173	18	8.3	18.2	0.6	42.4	20.2	10.1
M3	13.8 ± 1.1	5.1 ± 0.3	7.8 ± 0.1	4.5 ± 0.4	38.9 ± 5.0	3,919	78	2	33.7	4.9	0.4	48.9	5.1	7.0
M4	13.0 ± 1.1	5.5 ± 0.2	7.8 ± 0.1	10.8 ± 1.2	51.0 ± 5.3	6,948	81	0	40.5	1.9	0.1	51.0	2.2	4.3
M5	20.4 ± 0.9	5.4 ± 0.3	7.8 ± 0.1	7.3 ± 0.6	52.9 ± 4.9	4,026	87	3	69.0	2.4	0.0	19.8	1.1	7.7
M6	27.3 ± 0.8	5.8 ± 0.2	8.0 ± 0.0	5.5 ± 0.3	32.2 ± 6.1	26,568	219	14	79.2	6.8	0.1	9.2	0.9	3.8
M7	31.0 ± 0.6	6.4 ± 0.2	8.1 ± 0.0	5.9 ± 0.4	8.2 ± 1.0	111,195	306	31	50.9	35.2	4.2	5.1	1.8	2.8
M9	32.7 ± 0.4	6.3 ± 0.2	8.1 ± 0.0	5.4 ± 0.4	5.6 ± 0.5	75,951	329	57	50.2	10.0	10.6	3.8	17.0	8.4
M11	32.4 ± 0.5	6.1 ± 0.2	8.2 ± 0.0	5.0 ± 0.5	8.5 ± 1.7	48,242	278	22	42.8	8.3	28.0	4.6	4.7	11.6

Table 3. Comparative abundances[1] of 42 key taxa driving community composition at all 9 sites from 2005 − 2019.

Taxon	M1	M2	M3	M4	M5	M6	M7	M9	M11
ANNELIDA									
Capitella sp.		*	*	*	*	**	**	**	**
Dipolydora socialis (Schmarda 1861)	**	**		*	*	**	****	***	**
Fabricinuda trilobata (Fitzhugh 1983)		*				**	****	****	***
Fabriciola sp.							**	*	**
Glycera sp.		*		*	*	*	**	**	*
Glycinde sp.		*	*	*	**	**	**	**	**
Laeonereis sp.	***	***	*			*			
Laonome sp. A				*	*	***	***	***	***
Laonome sp. B					*	***	***	***	***
Lumbrineris sp.		*		*		*	***	***	***
Mediomastus californiensis Hartman 1944	**	*	*	*	***	****	***	***	***
Mediomastus sp.				*		***	***	***	**
Paraprionospio pinnata (Ehlers 1901)	*	*	**	*	**	**	**	*	*
Polydora sp.	**	*		*		*	***	***	**
Prionospio sp.	*	*		*		*	**	***	**
Pseudopolydora sp.	*	*		*	*	*	**	**	**
Scoloplos robustus Rullier 1964		*	*	*	**	**	*	*	**
Spiochaetopterus sp.	*	*	*	*	**	***	**	**	***
Sternaspis sp.					*	***	***	**	**
Syllis sp.						**	*		
Streblospio sp.	***	***	***	***	**	**	****	***	**
AMPHIPODA									
Americhelidium americanum (Bousfield 1973)						*	**	**	**
Ampelisca abdita Mills 1964	*	***	**	**	**	**	***	***	**
Apocorophium sp.	***	***		*		*	*	*	*
Caprella scaura Templeton 1836	*	*	*		*	*	**	***	***
Cerapus sp.	**	***		*	*	***	****	**	**
Ericthonius brasiliensis (Dana 1853)		*	*	*	*	*	**	***	***
Grandidierella bonnieroides Stephensen 1947	*	***	**	*	*	*	**	***	**
BIVALVIA									
Mulinia lateralis (Say 1822)	*	****	***	***	***	***	***	**	**
Mytilopsis leucophaeata (Conrad 1831)	**	****	***	*	*	*	*		*
Parvilucina sp.	*	*		*	*	*	***	**	*
Polymesoda sp.	**	***		*			*		
Rangia sp.	**	***	*	*	*				
Tellina spp.	*	***	*	*	*	*	***	**	**
GASTROPODA									
Acteocina canaliculata (Say 1826)	*	**	*	**		**	***	**	***
Assiminea succinea (Pfeiffer 1840)	***	***	*	*		*	*	*	*
Caecum pulchellum Stimpson 1851		*	*	*		*	**	****	***
Cerithium sp.	*	**	*				*	*	*
CNIDARIA									
Edwardsia elegans Verrill 1869	*	*					*	***	***
CUMACEA									
Cyclaspis varians Calman 1912	*	*	*	*		*	**	***	**
Oxyurostylis smithi Calman 1912		*			*	*	**	**	***
ISOPODA									
Amakusanthura magnifica (Menzies & Frankenberg 1966)	**	***		*		*	**	*	

[1] Based on total individuals: blank (absent, 0), * (rare, <50), ** (occasional, 51 − 500), *** (common, 500 − 5000), **** (abundant, >5000).

leucophaeata, *Polymesoda* sp. and *Rangia* sp.; the gastropod *Assiminea succinea*; and the isopod *Amakusanthura magnifica*. None of the taxa unique to particular sites were abundant enough to drive community composition.

Temporal Variation. An overall look at total infaunal abundance and taxonomic richness across the 9 sites revealed declines in both parameters in recent years. From 2015 to 2016, there was a loss of 76 taxa (Figure 2b and 2c) from several phyla. However, these were mostly rare and equaled just 877 individuals or 3.5% of the total abundance. In contrast, the subsequent decline in total abundance from 2016 to 2017 (Figure 2a) affected the most plentiful taxa, with a loss of 18,323 individuals or 36.5%. The proportions of major taxonomic groups were relatively stable across the years, apart from increased amphipod abundance in 2016, reflecting an October surge in *Cerapus* sp. at M7.

Discussion

Spatial Variation. The results from this study provide evidence of abiotic and biological distinction between the SLE and southern IRL and the inability for conditions at the convergence of the north and south forks of the St. Lucie River to support thriving infaunal communities characteristic of nearby sites. These distinctions effectively separate the sites into three zones that deviate slightly from those defined by geography: upper SLE (M1 and M2), middle SLE (M3 to M5) and southern IRL (M7 to M11), with M6 situated in a transition area. While further correlative analyses are needed, data suggest that salinity and the abundance of fine-grained sediments (along with other factors associated with grain size) are the major drivers of infaunal abundance, richness and community composition across these zones. Fine sediments of the mesohaline to polyhaline middle SLE hosted the lowest total abundance and richness of infaunal taxa, whereas the coarser sediments of the euhaline southern IRL hosted the highest. This is consistent with other studies on the biogeographical patterns of benthic infaunal macroinvertebrates. In a survey across 4 salinity zones and 3 sediment types in Nueces Bay, Texas, Mannino and Montagna (1997) found infaunal density and diversity to be negatively correlated with fine sediments and positively correlated with salinity. In a detailed investigation of infauna and sediment characteristics in the Cabras Lagoon (Sardinia, Italy), Magni and colleagues (2008) found that fine cohesive sediments <8μm affected community composition and led to reductions in infaunal abundance and biomass. Hale (2010) examined infaunal and abiotic environmental data from 614 sampling stations in U.S. Atlantic estuaries from northern Maine to Maryland. The results from this large analysis revealed that salinity was a major driver of infaunal community composition, especially in waters <18 ppt. The percentage of silt-clay in the sediments was an important secondary influencer of communities within regions. Finally, using data from the project presented herein, McKeon and coauthors (2015) examined bivalve communities in the southern IRL and SLE from 2005 to 2015 and found salinity to be the biggest predictor of species distributions. Bivalve diversity was highest in the euhaline IRL, while abundance peaked at the mesohaline to polyhaline SLE sites.
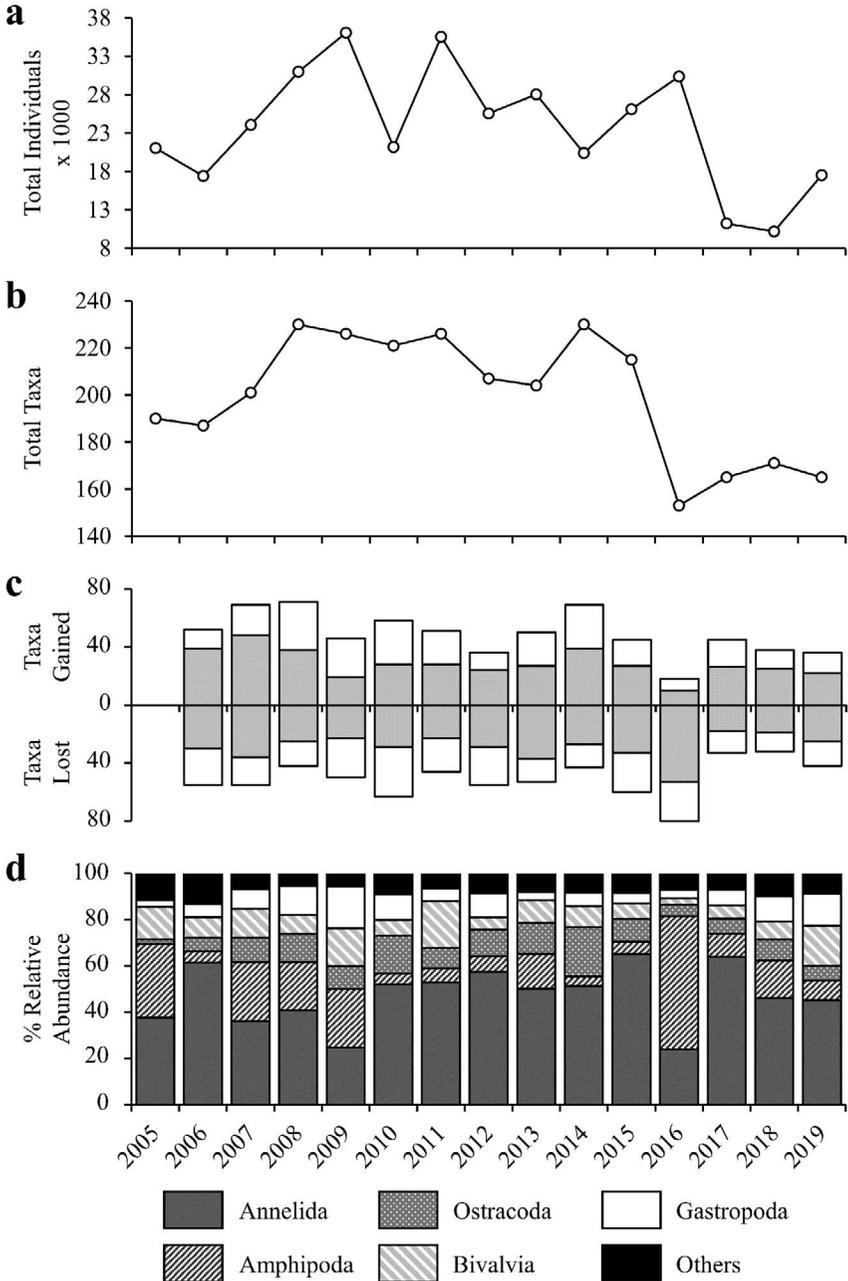
Figure 2. Annual benthic infaunal a) abundance, b) total taxa, c) taxa gained and lost from previous year (singletons = white, >1 individual = gray) and d) relative abundance of major taxonomic groups across all 9 monitoring sites from 2005 – 2019.

A closer look at the tolerances of taxa characteristic of the three zones identified in this study helps to interpret their distributions, which can be indicative of site health. The upper SLE supported taxa that are representative of freshwater and oligohaline environments elsewhere in Florida, including *Rangia* and *Polymesoda* that are commonly associated with low salinity areas in the Caloosahatchee Estuary (Barnes 2005). *Rangia* has been documented previously in the upper SLE where it comprised over 65% of the bivalve community at M1 (McKeon et al. 2015). While adult *Rangia* can survive salinities from 0 to 32 ppt (Anderson and Bedford 1973), their distributions are constrained by the narrower salinity tolerance of their larvae, between 2 and 10 ppt (Hopkins 1973, Christensen and Pyne 2020). Salinities in this range are typical at M1 and frequent at M2. Also abundant in the upper SLE is the bivalve *Mytilopsis leucophaeata*, with densities at M2 that can exceed 1,100 individuals L^{-1}. In a study of salinity as a barrier for the dispersal of bivalves transported on ship hulls, van der Gaag and colleagues (2016) found that *M. leucophaeata* favored salinities from 0.2 to 17.5 ppt and died after 14 days at salinities >20 ppt. It is therefore likely that the *M. leucophaeata* found rarely at the IRL sites are ephemeral.

The middle SLE sites had impoverished infaunal communities with only four common taxa (polychaetes *Mediomastus californiensis* and *Streblospio* sp., and bivalves *Mulinia lateralis* and *Mytilopsis leucophaeata*). While salinity tolerances limit the distributions of some of these taxa (e.g. *M. leucophaeata*), all are known opportunists that are otherwise tolerant of stressors like sedimentation, pollution and hypoxia (Pearson and Rosenberg 1978, Santos and Simon 1980, Dauer 1993, Cooksey and Hyland 2007). The middle SLE is the first to receive the brunt of upstream sediment-laden freshwater discharges from the St. Lucie River north fork, the C-23 and C-24 canals, and from Lake Okeechobee through the C-44 canal. Ungauged streams and surface runoff supply additional turbid water to the area – up to 37% of the total SLE freshwater input (Ji et al. 2007). Accumulation of fine-grained sediments likely facilitated other processes in the middle SLE that are harmful to benthic infauna. For example, fine-grained sediments are correlated with higher concentrations of metals (Chapman and Wang 2001) and organic content (Pearson and Rosenberg 1978). In low oxygen environments, toxic hydrogen sulfide is a metabolic byproduct of the bacteria that dominate fine organic-rich sediments (Diaz and Rosenberg 1995). Mean bottom dissolved oxygen in the middle SLE was lower than in the southern IRL. While concentrations were generally in the range that supports healthy biota, levels <3.0 mg L^{-1} were documented more at M3 than any other site, including a low of 0.61 mg L^{-1} in July 2007.

The thriving infaunal communities at the southern IRL sites contained taxa documented in detailed biodiversity assessments at the 1994 Biodiversity of the Indian River Lagoon Conference (Swain et al. 1995), including amphipods (Nelson 1995), isopods (Kensley et al. 1995), mollusks (Mikkelsen et al. 1995) and sipunculans (Rice et al. 1995). Many of species characteristic to M7 through M11 are also particularly abundant in other Florida benthic surveys where they are associated with clear euhaline waters and sandy sediments (Balthis et al. 2018,

Karlen et al. 2020), suggesting the taxa are indicative of healthy coastal environments. Two of the most abundant IRL taxa, the annelids *Fabricinuda trilobata* and *Mediomastus californiensis*, have never been recorded in the IRL Species Inventory (irlspecies.org), the clearinghouse for biodiversity data from the original assessments of the 1990s and other studies conducted to date. Pending taxonomic verification and cytochrome c oxidase subunit I (COI) gene barcoding, the records from this study will be added to that database.

Temporal Variation. A loss of 76 taxa occurred across the 9 monitoring sites from 2015 to 2016. While most of these losses represented rare taxa, densities fell for some typically abundant species as well, including *F. trilobata*, *M. californiensis* and *Laonome* sp. A and sp. B. Species losses and reductions in abundance were most pronounced at sites M6 to M9. A strong El Niño and wetter than normal conditions facilitated a bloom in July 2016 that was dominated by the toxic freshwater cyanobacterium *Microcystis aeruginosa*. The bloom started in Lake Okeechobee and extended out through the C-44 canal into the SLE, the southern IRL and the nearshore Atlantic Ocean when releases to control lake water levels began. Toxins including microcystins from *M. aeruginosa* and saxitoxins from other diazotrophic algae where detected from Lake Okeechobee east to the St. Lucie Inlet (Kramer et al. 2018). Blooms persisted into the fall, fueled by warm temperatures, long photoperiods, excess nitrogen and consistently low salinities that created hospitable conditions for *M. aeruginosa* at the coast (Lapointe et al. 2017, Kramer et al. 2018, RECOVER 2019). A transect survey of the bloom recorded a salinity of 6 ppt inside the St. Lucie Inlet in September 2016 (Kramer et al. 2018). *Microcystis* and microcystin production are unaffected at salinities up to 10 ppt and the alga can temporarily endure peaks as high as 17.5 ppt (Tonk et al. 2007). Studies on microcystin toxicity in aquatic organisms are scarce and are mostly limited to effects on fishes and zooplankton (Tencalla and Dietrich 1997, Jos et al. 2005, Gupta and Guha 2006, Shahmohamadloo et al. 2020). However, it is possible that toxins and other harmful constituents of the algal bloom played secondary roles in infaunal declines that were primarily driven by low salinity and sedimentation. While many taxa experienced declines during this time, numbers of the amphipod *Cerapus* sp. rose dramatically at M7 in October 2016. This may be explained by possible reductions in important amphipod predators such as fish and larger crustaceans (Virnstein et al. 1977, Nelson et al. 1982).

The drop in infaunal species richness in 2016 was followed by a nearly 37% decline in abundance in 2017. Hurricane Irma made landfall on September 10, 2017. Heavy rainfall caused daily nutrient and sediment-laden freshwater inflows to the SLE averaging 7,872 cfs from September 10 through October 12, 28% from Lake Okeechobee and 59% from the watershed (RECOVER 2019). The SLE is typically a stratified estuary where infauna at many sites experience mesohaline conditions even when freshwater inflows reduce surface salinities (Ji et al. 2007). However, persistently large freshwater flows can collapse the halocline and expose benthic organisms to abrupt decreases in salinity. This exposure can be even more sudden for infauna inhabiting coarser sediments because exchange and equilibration between interstitial and overlying water is faster in sands than in finer

sediments (Chapman and Wang 2001). These processes and the naturally lower freshwater tolerance of marine organisms inhabiting the southern IRL likely put infaunal communities at sites M7 and M9 at greater risk for salinity shock following not only Hurricane Irma, but also the freshwater releases from the previous year. For example, *Streblospio* sp. declined at M7 and M9 during 2016 and 2017. In an analysis of long-term trends in benthic macrofauna to climate variability in Lavaca-Colorado Estuary (Texas, USA), Pollack and colleagues (2011) documented that reductions in salinity due to river discharge were a major driver of changes in macrobenthic community structure, which included a drop in the abundance of *Streblospio benedicti*. The large population of *Cerapus* sp. at M7 also disappeared in 2017, which contributed to the overall decline. Although possibly tied to Hurricane Irma, it is more likely that this study captured the typical collapse of *Cerapus* following an unusually dense bloom, a cycle previously noted in the IRL and elsewhere (Boesch et al. 1976, Palmer et al. 2002).

Conclusions

Long-term monitoring of benthic infauna in the southern IRL and SLE documents biodiverse communities that vary dramatically across sites and have been adversely affected by major environmental events in recent years. Salinity and the abundance of fine-grained sediments appear to be major drivers of infaunal abundance, richness and community composition. These results provide a baseline for further analyses to better understand how organisms are affected by organic matter and contaminants, how community composition is driven by natural versus anthro-pogenically induced stressors, how functional diversity differs among sites, and how the biodiversity of these cryptic assemblages reflects that of the surrounding ecosystem. Also important is the need to turn results into recommendations, identifying dependable indicator species and selecting a benthic condition index from the many available (Borja et al. 2009, Ranasinghe et al. 2009, Dauvin et al. 2011, Veríssimo et al. 2011, Tweedley et al. 2014, Robertson et al. 2016) to transform this complex dataset into tangible targets for restoration success.

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