

Seagrass loss decreases abundance, diversity and composition of macrobenthic infauna in a Caribbean Bay

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Abstract

Seagrass meadows form extremely complex ecosystems in the coastal zone that are highly productive and sustain an abundant faunal community. This study compared the macrobenthic infaunal communities in William's Bay, Trinidad before and after a lush seagrass meadows dominated by *Thalassia testudinum* (Banks ex König) was extirpated. In 2007, *T. testudinum* leaf aerial productivity was $1.5 \pm 0.58 \text{ gm}^2 \text{ d}^{-1}$ and total biomass was $191 \pm 55.9 \text{ gm}^{-2}$, but by 2016 the bed had collapsed with zero productivity and biomass. To assess the macrobenthic infauna, five replicate cores were taken at six stations in 2007 and in 2016. Species richness, abundance and biomass all decreased from 2007 to 2016 coinciding with the loss of the seagrass meadows. This is likely due to fewer microhabitats and protection from predators provided by seagrass cover. Relative abundance of the main species groups remained unchanged; polychaetes accounted for 48% of the species in 2007 and 2016, amphipods accounted for 17% in both years, decapods for 12% and 15% in 2007 and 2016 respectively, non-segmented worms for 11% (2007) and 6% (2016), molluscs for 2% (2007) and 13% (2016), echinoderms for less than 1% and another 1% a small miscellaneous group. Specific composition within these groups differed; in 2007, carnivorous polychaete families Lumbrineridae, Nereididae and Orbiniidae dominated, while in 2016 deposit feeding polychaete families such as Opheliidae, Paraonidae, Capitellidae and Spionidae were more abundant. Epifaunal amphipoda dominated across both periods compared to infaunal tube-dwellers. This study demonstrated a shift in the main feeding guilds of polychaete communities while vegetated from carnivorous polychaetes to deposit feeding polychaetes upon disappearance of the seagrass meadows.

INTRODUCTION

Seagrass meadows enhance biodiversity, as they provide food for many invertebrates, larvae and juvenile fishes (Stoner, 1980) as well as habitats for a variety of permanent and temporary residents of varying ages, particularly among fish species (Tanner, 2003; Nakamura & Tsuchiya, 2008), polychaetes, amphipods, decapods and molluscs (Tanner, 2003). Seagrass material is consumed by a large number of faunal species and is important for sustaining the food web in tropical seagrass meadows. In Indo-Pacific meadows, large numbers of fauna such as crustaceans, copepods, amphipods, holothurids and herbivorous fish depend on seagrass material as a food source (Vonk, Christianen, & Stapel, 2008). Small crustaceans, like amphipods, copepods and isopods also graze on seagrasses (Boström & Mattila, 1999; Kharlamenko et al., 2008). The preservation of this seagrass-faunal relationship is key to maintaining biodiversity. When compared with nearby unvegetated areas, seagrass meadows contain a dense and strikingly rich assemblage of vertebrates and invertebrates. Epifaunal and infaunal abundance show positive correlation to the root rhizome mats and the plant canopy associated with seagrass meadows (Orth, Heck, & Montfrans, 1984).

Apart from biodiversity loss, change in species composition is also possible when seagrass beds are lost as observed in Gazi Bay, Kenya. Seagrass loss led to a shift toward larger bodied, bioturbating species, with a significant increase in mounds and burrows (Githaiga et al., 2019). These mounds and burrows may have played a role in facilitating predation and permitting higher sedimentary oxygen levels as the physical barriers of the dense seagrass canopy and rhizomes were removed (Githaiga et al., 2019). Seagrass removal also impacts total abundance, taxon richness and causes a large change in the proportional importance of different functional groups. Large molluscs, small crustaceans and worms are particularly vulnerable to seagrass removal (Githaiga et al., 2019).

The study of feeding guilds is important to understand spatial and temporal changes in benthic communities (Heip, 1992; Wieking & Kröncke, 2003) and their components such as polychaete assemblages (Muniz & Pires, 1999). Polychaete feeding guilds are based on the relationships between food particle sizes, feeding habits and the motility patterns associated with feeding (Fauchald & Jumars, 1979; Pagliosa, 2005).

Polychaetes in any benthic community display a wide range of feeding types, although in most soft-bottom communities, suspension (filter-feeders) and deposit-feeders (surface deposit-feeders and burrowers) dominate (Snelgrove & Butman, 1994). When polychaete feeding guilds are influenced by factors other than sediment type they represent a sensitive tool capable of detecting environmental change to a greater degree compared to density and diversity values (Domínguez Castanedo et al., 2012).

In Trinidad, the densest *Thalassia testudinum* dominated seagrass community was found in William's Bay in northwest Trinidad (Juman & Alexander, 2006). This area has been monitored since 2002. Between 2002 and 2016, seagrass density, biomass and areal productivity have generally decreased due to poor water quality associated with land-based anthropogenic activities, and land reclamation (Juman, 2012; IMA, 2016), until complete collapse in late 2016. The interactions between seagrass landscapes and their associated fauna are complex, difficult to predict and require more studies (Boström, Jackson, & Simenstad, 2006).

This study attempts to determine the effects declining seagrass health has on the macrobenthic fauna in terms of abundance, biodiversity, polychaete feeding guilds and amphipod microhabitats. It correlates macrobenthic fauna changes with declining seagrass health, deteriorating water quality, changes in sediment grain size and environmental pollution all of which affect benthic biodiversity (Stoffers et al., 1977; Hallock, 1988; Warwick, 1993; Warwick & Clarke, 1993; D'Croz et al. 2005), and compares results with a control site in Bon Acord Lagoon, where seagrass beds continue to thrive. This study also represents the first time benthic macroinvertebrate infauna have been studied in the seagrass beds of Trinidad and Tobago providing a useful baseline for comparison of macroinvertebrate communities in the future.

METHODOLOGY

Site Description

Trinidad and Tobago, located in the southernmost end of the Caribbean island chain (between 10° 02'-10° 50'N and 60° 55'-61° 56'W) on the continental shelf of South America, is immediately adjacent to the outflow of the Orinoco River. The country has a tropical climate with two distinct seasons (Henry, 1990). The dry season occurs between January and April, while the wet season extends from June to November. May and December are considered transitional months between the two seasons. Its marine ecosystems are influenced by discharge from South American Rivers, mainly the Orinoco River, while its terrestrial biota is largely South American. The tide is mixed, mainly semi-diurnal with a significant diurnal inequality (Kjerfve, 1981).

William's Bay, within the larger Carenage Bay on the northwest peninsula of Trinidad, is bordered by a popular recreational beach (1.1 km long) located at latitude 11°80'N; longitude 65°10' W (Fig. 1).

The bay was colonized by an extensive seagrass meadow dominated by *Thalassia testudinum*, that was home to a diversity of macrofaunal species including fishes such as seahorses, juvenile grunts and snappers, green turtles and invertebrates such as starfish, conch and urchins (Juman and Bejai, 2008). Since 2012, seagrass biomass and productivity in William's Bay had declined, coinciding with the development of tourism related infrastructure on the peninsula (IMA, 2016). By 2016, all the *Thalassia* dominated seagrass beds had disappeared from William's Bay.

Sampling methods

Water quality

Salinity was measured using an A366ATC hand held refractometer while temperature and dissolved oxygen were measured using the Sonde XLM 600 or YSI Meter. Water samples were collected with a Wildco Niskin 2.2 L Water Sampler at 1m depth. Total suspended solids (TSS) was determined according to the gravimetric (difference) method outlined in APHA, Greenberg, (1999). A known quantity of seawater was filtered through a pre-weighed Whatman glass fibre filter paper. The residue was dried for two hours at 105°C and re-weighed. The amount of nitrate, nitrite and ammonium in the water were determined following Grasshoff, Kremling, & Ehrhardt, (2007), while reactive phosphate was determined as per Strickland & Parsons (1972). Nitrites (N-NO₂), nitrates (N-NO₃), Ammonium (N-NH₄) and reactive phosphates (P-PO₄) in seawater were determined by reacting each anion with the respective complexing agents to form coloured solutions. UV/VIS spectroscopic (Perkin Elmer 552 A UV/VIS Spectrophotometer) analysis was used to quantify the anions present in the coloured solution. The detection limit for this method was 0.05 µM with a 5 cm cell.

Grain Size Analysis

Approximately 200–300g of sediment was collected from the sea floor (by scooping) for grain Size analyses of surface sediments at different sample stations by sieving following Folk, (1974) and Selim et al. (2012).

Seagrass Biomass

In 2007, four random cores (diameter 20 cm and depth 45-50cm) were taken with a PVC corer per station following the protocol of CARICOMP (2001). Coarse sorting was done on a sieve with a mesh of 1.5 mm and samples were washed with seawater. *T. testudinum* was then sorted into green leaves, non-green leaves and sheath, rhizome, roots and dead tissue and the green leaves were soaked in 5% phosphoric acid to remove epiphytes. The samples were then washed to remove salt and put onto pre-weighed foil and dried to constant weight at 60° C. Total biomass (summing the weight of all sorted tissues in a sample) is reported as grams of dry weight /m². In 2016, core samples were taken in the same sampling locations.

Areal productivity

In 2007, *T. testudinum* leaf aerial productivity was determined using a biomass accumulation method adapted from Zieman, (1974) and CARICOMP (2001). Six 10 x 20 cm (0.2 m²) PVC quadrats were randomly deployed (Plate 1). All the seagrass shoots in each of the quadrats were counted. Leaf growth was measured by marking all leaves of a leafy shoot a short distance above the green-white interface. All leaves on a shoot were marked with a single punch of a hypodermic needle (circumference = 5 mm) in the middle of the leaf blade. The marked seagrasses were allowed to grow for a minimum of seven days (range 7–17 days), after which they were harvested and taken back to the laboratory for analysis.

In the laboratory, all leaves on a short shoot were clipped at the point on the short shoot at which they were originally marked. The leaves were sorted into newly grown tissue and old standing crop, independent of whether the new growth was of new or standing leaves.

Leaves were cleaned of epiphytes by soaking in 5% phosphoric acid and then dried to constant weight at 60°C. Total dry weight was measured and these weights were then used to calculate areal productivity (P)

$$P \text{ (g dry wt m}^{-2} \text{ d}^{-1}\text{)} = \frac{(1 + 2) \times 50}{D} \text{ and}$$

where D is number of days; 1 = dry wt. of new grown tissue; 2 = dry wt. of old standing crop (CARICOMP, 2001). Density is expressed as number of shoots m⁻².

Seagrass areal productivity was measured four times per year; twice during the dry season (January to June) and twice during the wet season (July to December) while biomass was measured twice per year from 2007 to 2016, when surveys stopped due to the lack of seagrass; once in the dry season and once in the wet season.

Benthic Macrofauna

Six sites, previously sampled in the wet season (August) in 2007 by Daniel (2010, unpublished, Fig. 1), were resampled, during the dry (March) and wet (August) seasons in 2016. These periods represented states with (2007) and without seagrasses (2016). Sampling methods in both periods were the same.

Benthic macrofauna were collected using a hand held PVC corer (same as for seagrass biomass sampling). The National Geography in Shore Areas (NaGISA) protocol (Rigby, Iken, & Kato, 2007) for sampling seagrass infauna was used which involved immersing a 20 cm diameter corer to a depth of 10cm using a rubber bung at the top of the device to create a vacuum. A pre-sampling experiment was conducted by Daniel (2010, unpublished, Fig. 2) to determine the number of replicates required to accurately determine benthic composition per site. The cumulative frequency curve which measured number of species vs number of replicates suggested five replicates would be adequate

Core samples were sieved in the field using a 0.5mm mesh screen. Samples were stained with Rose Bengal to distinguish between dead and living invertebrates. Dead organisms were discarded while the living ones were used for analysis. Fauna collected was preserved with a 10% formalin-seawater mixture. Benthic samples were sorted by hand. Macroinvertebrates were identified to the lowest possible taxonomic level using the following keys: The Polychaete worms (Fauchald, 1977), Aquatic Oligochaeta (Brinkhurst, 1971), Intertidal and shallow water amphipods (Paz-Ríos, Simões, & Ardisson, 2013). Accepted taxa were checked at World Register of Marine Species www.marinespecies.org. Dry weights of the macrofauna were determined by drying at 60°C for 24 hours.

The null hypothesis tested was that there was no significant difference between benthic macrofaunal communities associated with seagrass beds, and the communities found after the disappearance of seagrass beds. Statistical tests employed to test this null include: Posthoc Bonferroni corrected t-tests, Pearson's Correlation, Spearman's Rank correlation using Microsoft EXCEL 2016 and SIMPER analysis using PRIMER 6 software.

RESULTS

Decline in Seagrass

Water quality (physical and nutrients) and biological parameters measured for the different sampling periods are provided in Table 1. From 2007 to 2016, there was a drastic decline in *Thalassia testudinum* aerial productivity and total biomass. *T. testudinum* beds were completely decimated by 2016 in terms of both growth (Fig. 3a) and biomass (Fig. 3b), which showed steady declines from 2006 to 2016.

Water Quality

The water quality of the William's Bay area was measured from 2006 to 2016 at least once per year in the William's Bay area at two stations C and F in Fig. 1 (See Appendix A). Pearson's Correlation was performed with seagrass aerial productivity, biomass measurements against various water quality parameters (Table 1).

Table 1
p values for Pearson Correlation performed on seagrass growth and biomass with water quality parameters (Nitrates, NO₃-N; Nitrites, NO₂-N; Ammonium, NH₃-N; Reactive Phosphates, RxPO₄ and Total Suspended Solids, TSS) for stations C and F

		NO ₃ -N	NO ₂ -N	NH ₃ -N	RxPO ₄	TSS
Station C	Growth	-0.282	-0.371	0.124	0.069	0.003*
	Biomass	-0.111	-0.349	0.206	0.081	-0.048*
Station F	Growth	0.013*	0.084	0.211	0.324	-0.276
	Biomass	0.281	-0.209	-0.023*	0.247	-0.12

Station C showed a significant correlation between growth and Total Suspended Solids (TSS) ($p < 0.05$) and a significant negative correlation between biomass and TSS. Station F showed a significant correlation between growth and nitrates (NO₃-N) ($p < 0.05$) and a significant negative correlation between biomass and ammonium (NH₃-N). There was very little growth of other species (*Halodule wrightii*) and macroalgae, and the seafloor was mostly exposed. Small patches of dead *T. testudinum* rhizomes remained below ground.

Dissolved oxygen concentration, temperature and TSS levels generally increased from 2007 to 2016 (Table 2). Salinity was lower during the wet seasons while pH did not change with season. All parameters were measured between mid-morning to mid-day. Across all sampling events, nitrate, nitrite, and reactive phosphate concentrations remained fairly constant, however ammonium concentration increased in 2016 by at least 6 folds but remained below the USEPA (1995) guideline limit of 1.43 μM which indicates chronic toxicity to aquatic life. Total suspended solids in the water column increased from 2 mg l⁻¹ in 2007 (wet season) to 16.6mg l⁻¹ (dry season) and 11.9 mg l⁻¹ (wet season) in 2016 (Table 2).

Table 2
Average values (\pm SD) of physio chemical parameters of water quality measured at William's Bay, Trinidad in 2007 and 2016. (N = number of samples)

Parameters	Wet season 2007	Dry season 2016	Wet Season 2016
Dissolved oxygen (mg l^{-1})	3.41 ± 0.48 (N = 6)	5.84 ± 0.26 (n = 6)	6.33 ± 0.54 (N = 6)
Temperature °C	25.95 ± 0.23 (N = 6)	27.10 ± 0.32 (n = 6)	29.48 ± 0.20 (N = 6)
Salinity (‰)	30.56 ± 0.19 (N = 6)	35.14 ± 0.12 (n = 6)	19.29 ± 0.13 (N = 6)
pH	8.62 ± 0.48 (N = 6)	8.08 ± 0.03 (n = 6)	7.91 ± 0.10 (N = 6)

In 2007, the sediment grain size was classed as slightly gravelly sand using Folk (1974), with the exceptions of Stations E and F (Table 3). In 2016, this classification changed to fine sand for the majority of stations with the exception of station E (Table 3). Notably, mud percentages decreased while sand percentage increased.

Table 3
Grain size percentages and Folk Classification for stations sampled in 2007 and 2016

Station	A	B	C	D	E	F	
<i>Sediment Composition (%)</i>							
2007	Gravel	4	3.4	4	15.5	0.1	1.9
	Sand	95.2	93.5	92.8	76.3	99.6	83.7
	Mud	0.8	3.1	3.2	8.2	0.3	14.5
	Folk Classification	slightly gravelly sand	slightly gravelly sand	slightly gravelly sand	slightly gravelly sand	gravelly sand	medium sand
2016	Gravel	0	0	0.8	0.3	4.2	1.4
	Sand	100	99.9	96.9	99.6	95.8	98.5
	Mud	0	0.1	2.3	0.1	0	0
	Folk Classification	fine sand	fine sand	fine sand	fine sand	medium sand	fine sand

Chi squared test showed there was no significant difference ($p < 0.001$) between the sediment composition for 2007 and 2016. Spearman's rank correlation showed no significant difference ($p < 0.05$) between number of species collected and gravel percentage for 2016 only (Table 4). The null hypothesis was rejected for the 2007 data.

Table 4
Spearman's Rank correlation comparing grain size to abundance m^{-2} , biomass m^{-2} and number of species

	2007 gravel	2007 sand	2007 mud	2016 gravel	2016 sand	2016 mud
number of species	0.461	0.957	0.623	0.024*	0.111	0.594
abundance m^{-2}	0.084	0.329	0.544	0.173	0.208	0.954
biomass m^{-2}	0.957	0.329	0.208	0.173	0.208	0.954

Polychaetes

In 2007, polychaetes were the most dominant taxon accounted for 52% of the total number of species. *Leitoscoloplos fragilis* was the most dominant polychaete (Verrill, 1873) with 98 individuals. Polychaetes were also the most dominant taxon for both seasons in 2016 accounting for 47% of all species in the dry season and 54% in the wet season. The most dominant polychaete for the dry season was *Aricidea (Acmira) taylori* Pettibone, 1965 (128 individuals) with *Armandia agilis* (Andrews, 1891) (356 individuals) being the most dominant for the wet season.

The feeding habits of the polychaetes were classified according to Fauchald and Jumars (1979) and Jumars et al. (2015) and presented in Table 5.

Table 5
Comparison of polychaete families between 2007 and 2016 according to their feeding guilds.

Family	Species 2007	Species 2016	Feeding Habits
Aphroditidae	<i>Aphrodita c.f. acuelata</i>		carnivore
Capetillidae	<i>Capetilla sp. A</i>		deposit feeders
	<i>Capitella capitata</i>	<i>Capitella capitata</i>	deposit feeders
	<i>Capitellides jonsei</i>		deposit feeders
	<i>Heteromastus filiformis</i>	<i>Heteromastus filiformis</i>	deposit feeders
	<i>Leiocapitella sp. A</i>	<i>Leiocapitella sp A</i>	deposit feeders
	<i>Mediomastus sp.</i>	<i>Mediomastus sp.</i>	deposit feeders
	<i>Notomastus latreicus</i>	<i>Notomastus latericeus</i>	deposit feeders
	<i>Notomastus sp. A</i>		deposit feeders
		<i>Notomastus filiformis</i>	deposit feeders
Cirratulidae	<i>Caulleriella c.f. alata</i>		deposit feeders
	<i>Caulleriella sp.</i>		deposit feeders
	<i>Caulleriella sp. A</i>		deposit feeders
	<i>Chaetozone setosa</i>		deposit feeders
	<i>Chaetozone sp. A</i>		deposit feeders
	<i>Chone c.f. americana</i>		deposit feeders
	<i>Tharyx sp.A</i>		deposit feeders
	<i>Tharyx sp. B</i>		deposit feeders
Dorvellidae	<i>Dorviella rubra</i>		carnivore
	Genus C		carnivore
	<i>Schistomeringos pectinata</i>		carnivore
	<i>Dorvillea sp. A</i>	<i>Dorvillea sp. A</i>	deposit feeders
Eulepethidae	<i>Grubeulepis mexicana</i>		carnivore
Glyceridae	<i>Glycera sp. A</i>	<i>Glycera sp.A</i>	carnivore
	<i>Glycera sp. B</i>		deposit feeders
Goniadidae	<i>Goniada littorea</i>		carnivore
	<i>Goniada sp. A</i>	<i>Goniada sp. A</i>	carnivore
Hesionidae	<i>Podarke sp. A</i>	<i>Podarke sp.A</i>	carnivore
Lumbrinidae	<i>Lumbrineris brevipes</i>		omnivore
	<i>Lumbrineris coccinea</i>		omnivore
	<i>Lumbrineris ernesti</i>		omnivore
	<i>Lumbrineris januarii</i>	<i>Lumbrineris januarii</i>	omnivore
	<i>Lumbrineris latreilli</i>	<i>Lumbrineris latreilli</i>	omnivore
	<i>Lumbrineris sp. A</i>		omnivore
	<i>Lumbrineris sp. B</i>		omnivore
	<i>Lumbrineris sp. C</i>		omnivore
	<i>Lumbrineris taylori</i>		omnivore
	<i>Lumbrineris tenuis</i>		omnivore
	<i>Ninoe sp. A</i>		omnivore
Magelonidae	<i>Magelona pettiboneae</i>		deposit feeders

Family	Species 2007	Species 2016	Feeding Habits
	<i>Magelona sp. A</i>	<i>Magelona sp. A</i>	deposit feeders
	<i>Magelona sp. B</i>		deposit feeders
Maldanidae	<i>Asychis elongatus</i>		deposit feeders
	<i>Axiothella sp. A</i>	<i>Axiothella sp.A</i>	deposit feeders
	<i>Euclymene sp. A</i>		deposit feeders
	<i>Johnstonia c.f. kynsa</i>		deposit feeders
	<i>Johnstonia duplicata</i>		deposit feeders
	<i>Maldane sp. A</i>	<i>Maldane sp.A</i>	deposit feeders
	<i>Maldane sp. B</i>		deposit feeders
	<i>Maldane sp. C</i>		deposit feeders
Nereididae		<i>Lumbrineris ernesti</i>	deposit feeders
	<i>Ceratonereis longicirrata</i>		omnivore
	<i>Ceratonereis mirabilis</i>		omnivore
	<i>Ceratonereis versipedata</i>	<i>Ceratonereis versipedata</i>	omnivore
	<i>Nereis falsa</i>		omnivore
	<i>Nereis lamellosa</i>	<i>Nereis lamellosa</i>	omnivore
	<i>Nereis pelagica</i>	<i>Nereis pelagica</i>	omnivore
	<i>Nereis sp. A</i>	<i>Nereis sp.A</i>	omnivore
Onuphidae	<i>Onuphis sp. A</i>	<i>Onuphis sp.A</i>	deposit feeders
	<i>Onuphis sp. B</i>		deposit feeders
	<i>Ramphobrachium sp. A</i>		deposit feeders
Opheliidae	<i>Armandia agilis</i>		deposit feeders
	<i>Armandia maculata</i>	<i>Armandia maculata</i>	deposit feeders
	<i>Armandia sp. A</i>		deposit feeders
Orbinidae	<i>Leitoscloplos fragilis</i>		deposit feeders
	<i>Leitoscloplos robustus</i>	<i>Leitoscloplos robustus</i>	deposit feeders
	<i>Leitoscloplos sp. A</i>		deposit feeders
	<i>Leitoscloplos sp. B</i>		deposit feeders
	<i>Scoloplos fragilis</i>		deposit feeders
	<i>Scoloplos rubra</i>	<i>Scoloplos rubra</i>	deposit feeders
	<i>Scoloplos sp. A</i>		deposit feeders
	<i>Scoloplos sp. B</i>		deposit feeders
	<i>Scoloplos texana</i>		deposit feeders
	<i>Naineris sp. A</i>		deposit feeders
	<i>Phylo felix</i>		deposit feeders
Paeronidae	<i>Aricidea fragilis</i>		deposit feeders
	<i>Aricidea (Acmira) taylori</i>	<i>Aricidea (Acmira) taylori</i>	deposit feeders
	<i>Aricidea philbinae</i>		deposit feeders
	<i>Aricidea pseudoarticulata</i>	<i>Aricidea pseudoarticulata</i>	deposit feeders
	<i>Aricidea sp. A</i>		deposit feeders
	<i>Aricidea sp. B</i>	<i>Aricidea sp.B</i>	deposit feeders

Family	Species 2007	Species 2016	Feeding Habits
Phyllodocidae	<i>Eumida sanguinea</i>		carnivore
	<i>Eumida sp.</i>	<i>Eumida sp.</i>	carnivore
Pilargidae	<i>Sigambra tentaculata</i>	<i>Sigambra tentaculata</i>	carnivore
Poecilochaetidae	<i>Poecilochaetus johnsoni</i>		suspension feeder
Polynoidae	<i>Lepidasthenia sp. A</i>	<i>Lepidasthenia sp.A</i>	carnivore
	<i>Polynoidae sp. A</i>	<i>Polynoidae sp.A</i>	carnivore
Sabellidae	<i>Sabella melanostigma</i>		filter feeders
	<i>Megalomma sp. A</i>	<i>Megalomma sp. A</i>	suspension feeder
	<i>Sabella sp. A</i>	<i>Sabella sp. A</i>	suspension feeder
Spionidae	<i>Misrospio cirrifera</i>		deposit feeders
	<i>Prionospio heterobranchia</i>	<i>Prionospio heterobranchia</i>	deposit feeders
	<i>Prionospio (Apoprionospio) pygmaea</i>		deposit feeders
	<i>Prionospio (Minuspio) cirrifera</i>	<i>Prionospio (Minuspio) cirrifera</i>	deposit feeders
	<i>Prionospio (Minuspio) sp. A</i>		deposit feeders
	<i>Spio armata</i>	<i>Spio armata</i>	deposit feeders
	<i>Spio pettiboneae</i>		deposit feeders
Syllidae	<i>Trypanosyllis vittigera</i>		carnivore
	<i>Exogene atlantica</i>		deposit feeders
	<i>Exogene sp.A</i>		deposit feeders
	<i>Exogene sp. B</i>		deposit feeders
	<i>Pionosyllis sp.A</i>		deposit feeders
	<i>Pionosyllis sp. B</i>		deposit feeders
	<i>Pionosyllis vittigera</i>		deposit feeders
Terebellidae	<i>Loimia sp. A</i>		Filter feeders
	<i>Loimia medusa</i>	<i>Loimia medusa</i>	suspension feeder
Trichobranchidae		<i>Trichobranchidae sp. A</i>	suspension feeder

Deposit feeders accounted for the largest number of polychaete taxa with 65 in 2007 and 21 in 2016. The deposit feeding families Cirratulidae, Orbiniidae, Maldanidae and Syllidae were well represented in 2007. The number of species for each of these families showed a marked decrease in 2016. Eighteen (18) omnivorous species were recorded in 2007 and 6 in 2016. The family Lumbrineridae was well represented in 2007 with 11 different species. This number fell to 2 in 2007. Fifteen (15) carnivorous polychaetes were recorded in 2007 and 7 in 2016. Two (2) filter feeding species were found in 2007 and 0 were recorded in 2016. The same number of suspension feeder species (4) were found in both periods.

Amphipods

Amphipods were the most abundant organisms, accounting for 49% (1,779 individuals) of all individuals collected in 2007 (N = 3,604 individuals), with *Erichthonius brasiliensis* (Dana, 1853) as the most abundant species with 607 individuals. During the dry season of 2016, amphipods were the second most abundant representing 30% of all organisms, with *Eudevenopus honduranus* (Thomas & J.L. Barnard, 1983) being the most abundant (204 individuals). During the wet season in 2016, amphipod abundance however fell to 7%, with *E. honduranus* as the most abundant (43 individuals). Amphipod abundance was higher in 2007 compared to the dry season and wet season in 2016.

In terms of number of species, Amphipoda accounted for 11% of all species collected in 2007 and 17% in 2016. Twenty-two (22) amphipod species were found in 2007 while 12 species were recorded in 2016 (Table 4). Twelve species were common to both sampling periods. Their microhabitats were classified according to Bousfield (1973) (Table 6). Fourteen (14) species had epifaunal microhabitats of which 7 were domicolous (tube dwelling) and 6 were free living. Six (6) species were infaunal, 1 was motile, 1 commensal and 1 the microhabitat was undetermined. Aoridae was the best represented family in 2007 with 4 species. It was also the best represented in 2016 with 3 different species.

Table 6
Comparison of amphipod families between 2007 and 2016 according to their microhabitats

Family	2007 species	2016 species	Microhabitat
Ampeliscidae	<i>Ampelisca holmesi</i>	<i>Ampelisca holmesi</i>	infaunal tube builder
	<i>Ampelisca parapanamensis</i>	<i>Ampelisca parapanamensis</i>	infaunal tube builder
Amphilochidae	<i>Gitanopsis sp. A</i>		epifaunal free living
	<i>Apolocus sp. A</i>		epifaunal free living
Aoridae	<i>Grandidierella bonnieroides</i>	<i>Grandidierella bonnieroides</i>	epifaunal
	<i>Bemlos longicornis</i>	<i>Bemlos longicornis</i>	epifaunal domicolous
	<i>Bemlos unicornis</i>	<i>Bemlos unicornis</i>	epifaunal domicolous
	<i>Bemlos sp.A</i>		epifaunal domicolous
Bateidae	<i>Batea catherinensis</i>	<i>Batea catherinensis</i>	epifaunal free living
Caprellidae	<i>Caprella scaura</i>	<i>Caprella scaura</i>	epifaunal free living
Corophiidae	<i>Laticorophium baconi</i>		infaunal free burrower
	<i>Cerapus sp.A</i>		motile tube
Euceridae	<i>Nasogenia c.f. yucatanensis</i>		n/a
Gammaridae		<i>Gammarus sp.A</i>	epifaunal free living
Ischyroceridae	<i>Erichthonius sp.A</i>		epifaunal domicolous
	<i>Erichthonius punctatus</i>		epifaunal domicolous
	<i>Erichthonius sp. A</i>		epifaunal domicolous
Leucothoidae	<i>Leucothoe sp. A</i>	<i>Leucothoe sp.A</i>	commensal
Lysianassidae	<i>Lysianassa c.f. hummelinki</i>	<i>Lysianassa c.f. hummelinki</i>	infaunal free burrower
Megaluropidae	<i>Gibberosus myersi</i>	<i>Gibberosus myersi</i>	infaunal
Melitidae	<i>Melita c.f. planiterga</i>	<i>Melita planaterga</i>	epifaunal free living
Neomegamphopidae	<i>Neomegamphopus c.f. hiatus</i>		epifaunal domicolous
Platyschnopidae	<i>Eudevenopus honduranus</i>	<i>Eudevenopus honduranus</i>	infaunal

A total of 104 polychaete species were recorded in 2007 (Table 7). This number fell to 38 in 2016. Thirty-five similar species were found across both sampling periods with 69 found in 2007 alone and 3 found in 2016 alone. Amphipod abundance and biomass decreased from the 2016 dry season to the 2016 wet season while the number of species remained the same (Table 7). The 2007 wet season values were higher than both of the 2016 seasons.

Table 7

Comparison of major taxa found in William's Bay between the 2007 and 2016 sampling periods according to number of species, species density (no. m⁻²) and biomass (g m⁻²)

Taxonomic grouping	2007 wet			2016 dry			2016 wet		
	No. of species	Species density (no. m ⁻²)	Biomass (g m ⁻²)	No. of species	Species density (no. m ⁻²)	Biomass (g m ⁻²)	No. of species	Species density (no. m ⁻²)	Biomass (g m ⁻²)
Amphipods	22	99624	40.376	12	28000	0.616	6	6608	0.112
Crustaceans	21	7504	166.096	11	1344	0.056	6	1344	10.248
Echinoderms	4	672	1463.336	1	1848	4.48	1	896	5.712
Mollusca	13	4312	1288.504	9	18592	1697.64	5	31416	2672.936
Non segmented worms	25	10864	107.8	5	13048	6.944	4	7000	2.632
Polychaetes	106	61320	461.328	34	36680	31.584	26	48272	37.072
Miscellaneous	6	560	149.576	0	0	0	0	0	0
Other Arthropods	9	16968	3.192	0	0	0	0	0	0
TOTAL	206	201824	3680.208	72	99512	1741.264	48	95536	2728.712

Macrofaunal biomass from 2007 ranged from 234 g m⁻² to 1709 g m⁻² (mean density = 608.52 g m⁻²). The biomasses from 2016 ranged from 11.06 g m⁻² to 605.44 g m⁻² (mean density = 369.57 g m⁻²) for the dry season and 0 g m⁻² to 820.84 g m⁻² (mean density = 451.21 g m⁻²) for the wet season. A large proportion of the biomass is attributable to Mollusca, specifically *D. punctata*, a suspension-feeding bivalve, in both 2007 and 2016 (Table 7). In 2007, higher numbers of echinoderms also contributed to an increased biomass. While echinoderms had the largest biomass in the 2007 samples, there was a marked decrease in 2016 (Table 7).

Polychaete species decreased greatly in biomass from 2007 to 2016 (Table 7). Polychaete biomass was the greatest in 2007 with marked decreases for both dry and wet seasons in 2016. Mollusca biomass however, showed a marked increase from 2007 to 2016.

Number of species, abundance per square metre and biomass all decreased from 2007 to 2016 (Table 8). Station A showed a notable decline during this period. For the 2016 sampling periods, there was a reduction in the total number of species and abundance when compared to 2007 for both seasons (Table 8).

Table 8

Comparison of stations sampled in William's Bay among the three sampling events according to number of species, species density (no. m⁻²) and Biomass (g m⁻²)

Station	2007 wet			2016 dry			2016 wet		
	No. of species	Species density (no. m ⁻²)	Biomass (g m ⁻²)	No. of species	Species density (no. m ⁻²)	Biomass (g m ⁻²)	No. of species	Species density (no. m ⁻²)	Biomass (g m ⁻²)
A	110	24335	28640	16	5389	1048	3	611	6
B	134	26224	13136	18	6945	619	15	3889	1745
C	151	50726	24859	33	11834	16406	19	16168	22635
D	92	15779	25109	28	14168	28898	28	31558	45967
E	127	55171	95733	38	26780	33905	30	23113	42103
F	140	28002	16985	48	33614	15868	31	19446	39150
Average	125	33373	34077	30	16126	20696	21	15798	25268
std. dev.	21	16952	30748	12	11318	13763	11	11729	20508

Lowest species density was observed in Station D for 2007 and Station A for 2016 wet and dry seasons. Station B had the lowest biomass level in 2007 and the 2016 dry season, while station A had the lowest biomass for the wet season. Differences in density and biomass were observed spatially between the western (A-C) and eastern (D-F) stations (Table 6). SIMPER analysis confirmed that the variations observed between the western and eastern stations were due to the dominance of different species. Polychaetes *A. taylora* and *A. agilis* dominated at Stations A and B respectively and the bivalve

Diplodonta punctata (Say, 1822) dominated at Stations D to F. Polychaete abundance was highest at Station D, for both seasons in 2016. The low macrofaunal biomasses found at Stations A and B in 2016, may have been due to the higher abundance of opportunistic species present at these two stations such as *Capitella capitata* (Fabricius, 1780) and the small number of bivalves that were recorded. Stations A and B are located toward the western most section of William's Bay which is a popular bathing area.

A total of 198 species were recorded in 2007 and 80 in 2016. Sixty-three species were common to both sampling periods, 17 species were found in 2016 alone and 135 were found in 2007 alone. P-values for Post-hoc Bonferroni corrected t- tests were performed on the three sampling periods for number of species, biomass and number of organisms per square metre. The results of these tests are presented in Table 9.

Table 9
P values for post-hoc Bonferroni corrected Two-tailed t-tests comparing number of species, biomass/g and abundance/m² for 2007 and 2016 sampling seasons

	2007 wet	2016 dry	2016 wet
No. of species*			
2007 wet		< 0.001	< 0.001
2016 dry	< 0.001		> 0.05
2016 wet	< 0.001	> 0.05	
Biomass**			
2007 wet		< 0.05	< 0.05
2016 dry	< 0.05		> 0.05
2016 wet	< 0.05	> 0.05	
Species Density **			
2007 wet		< 0.05	< 0.05
2016 dry	< 0.05		> 0.05
2016 wet	< 0.05	> 0.05	

***T value = 2.23**

****T value = 2.57**

Number of species, biomass and species density were all significantly different ($p < 0.001$) between 2007 and the dry season and the wet season of 2016. There were no significant differences between the wet and dry seasons in 2016.

Comparison with BAL

Thalassia beds in Bon Accord Lagoon (BAL), serves as a control site for comparison with those sampled in William's Bay Chaguaramas (Fig. 4).

Six sites were sampled using the CARICOMP methodology in 2007 (Daniel, 2010 unpublished). These same sites were resampled in 2018. During this time, seagrass beds continued to flourish within the BAL. A total of 130 different species and 64,782.96 individuals per square metre were counted for Bon Accord Lagoon during 2007 (See Appendix B for station location and table of results comparison for 2007 and 2018). The 2018 season recorded 107 species and 82,062.12 individuals/ m². However, the 2007 sampling event recorded the higher biomass (2210.68 g/m²) when compared with the 2018 wet (1177.59 g/m²). Analysis of Variance (ANOVA) showed significance difference 2007 and 2018 wet season ($p < 0.05$). The average Shannon-Wiener Diversity Index for 2007 was calculated as 2.18, whereas the average Shannon Wiener Diversity Index for 2018 was recorded as 2.63. The benthic communities continued to flourish as the seagrass population remained viable throughout this period.

DISCUSSION

Seagrass beds provide critical ecosystem services including the provision of food and shelter for a host of benthic, epiphytic and pelagic organisms (Hutchings et al., 1991; Schneider & Mann, 1991; Edgar & Robertson, 1992; Larkum, Orth, & Duarte, 2006; Bell, Fonseca, & Stafford, 2006). In Florida Bay, and other areas in the Northern Caribbean, seagrass beds are major nursery areas and lifetime habitats for a number of species, including some commercially important species: grunt, groupers, snappers, sea bream, pink shrimp (*Penaeus sp.*) and spiny lobster, *Panulirus argus* (Latreille, 1804; Robblee, 1989; Sogard et al., 1989; Thayer and Chester, 1989; Van der Velde et al., 1992). Many of these species feed on various forms of marine macrofauna associated with seagrass beds. Where seagrasses are present, the feeding guilds of macrobenthic faunal communities differ to areas where they are absent (Han, Han, Zheng, & Han, 2017)

When the benthic communities in William's Bay are compared to those in BAL there is a stark difference in terms of diversity, abundance and number of species. The benthic community at BAL showed increased abundance, diversity and number of species over a similar time period. This supports the hypothesis that seagrasses are influential in the structure and composition of benthic communities leading to increased diversity and abundance and its loss leads to reduction in these parameters. It is likely these effects are secondary through its influence on local hydrodynamics, food availability and quality and protection from predators (Alsaffar et al., 2020).

Not all studies agree with the view that seagrass canopy cover leads to increased diversity and abundance in benthic fauna (Attrill, Strong, & Rowden, 2000; Lee, Fong, & Wu, 2001; Nakamura & Sano, 2005; Barrio Froján et al., 2009; Barnes & Barnes, 2014). However, this study demonstrates a clear decrease in the number of taxa, species abundance and biomass of benthic macrofaunal communities at the same location, which was vegetated and then unvegetated due to the decimation of the seagrass meadow. Several authors have noted that macrofaunal densities at sites vegetated by seagrasses were higher than nearby unvegetated sites (Thayer et al. 1975; O'Gower & Wacasey, 1967; Orth, 1973; Santos & Simon, 1974) however, all except Santos and Simon (1974) found sediment granulometry correlated with macrophyte biomass.

Chi squared test showed no significant difference between the sediment composition in 2007 and 2016. Data presented here show that abundance, diversity and species number of the macrobenthic community may be a function of macrophyte cover and not fine sediments. The disappearance of the seagrass beds would favour the increase in deposit feeders as they usually find it difficult to flourish in heavily vegetated habitats due to heavy rhizome mats, and show lower abundances (Stoner, 1980; Cardoso et al., 2004). However, the effects of sediment granulometry and seagrass cover on benthic communities are difficult to disaggregate therefore it is impossible to state for sure whether observed changes on the benthic community are a direct result of the loss of seagrass meadows. It would appear however, that water quality parameters such as total suspended solids, nitrates and ammonium concentrations negatively impacted the seagrass community as significant negative correlations were found between these parameters and seagrass productivity and biomass at the two stations. Nutrient over-enrichment of coastal waters has been cited as the main reason for seagrass loss (Orth & Moore 1983, Short & Wyllie-Echeverria 1996).

As the seagrasses gradually disappeared from 2007 to 2016, deposit-feeding polychaetes would have found a favourable environment hence a greater proliferation of these organisms. A common assumption is that deposit-feeders are abundant in muddy habitats while suspension feeders dominate in sandy habitats (Gray, 1981). Mud percentages decreased from 2007 to 2016; however, the classification of the sediment changed from coarser, gravelly sand to finer sand (Table 2). This supports the theory that deposit feeders prefer finer sediments. The suspension feeders did not appear to be affected as both species were still present in 2016. Some species can modify their trophic habits in response to food availability, and also their ability to colonize bottoms with high sediment mobility, for example, spionids, (Maurer, Leathem, & Menzie, 1981). Not all species are associated with a single sediment type, but their trophic organization can relate to associated factors such as organic content and granulometric properties of sediments (Snelgrove & Butman, 1994).

Several epifaunal amphipod species were no longer present in 2016 such as *E. brasiliensis* and *Neomegamphopus hiatus* (Barnard & Thomas, 1987) (Table 6). The number of epifaunal species decreased from 13 to 7 across both sampling periods while infaunal species remained the same with the exception of *Laticorophium baconi* (Shoemaker, 1934) which was present in 2007 but disappeared in 2016. Stoner (1979) showed that for amphipods, seasonal abundance patterns were related to reproductive seasonality and abundance of predatory fish. Limited experimental evidence suggests that some amphipods actively seek certain vegetation (Stoner, 1980) and that these species, are more vulnerable to predation when outside the protection of the seagrass blades (Nelson, 1979; Coen et al., 1981; Stoner, 1980).

Epifaunal species would be more protected from predation among the fronds of *Thalassia testudinum* leaves. Upon disappearance of the seagrasses, their numbers would naturally decrease as protection is no longer available. The top three most abundant species in 2016 were two infaunal species *E. honduranus* and *Gibberosus myersi* (McKinney, 1980) along with the epifaunal *Grandidierella bonnieroides* Stephensen, 1957. Traditionally, infaunal species have a harder time with dense rhizome mats although this does not appear to be the case as the number of infaunal species remained relatively constant. Infaunal species appear to have been less affected by the disappearance of seagrasses resulting in small shifts in community composition. Apart from changes in sediment type, location played an important role in the distribution of the macrobenthic community.

Stations A and B are located in popular bathing areas of William's Bay. Both of these stations showed marked decreases in number of macrofaunal species, abundance and biomass compared to the other four stations sampled (Table 8). Continuous disturbance by beachgoers may negatively affect the benthic fauna leading to there being smaller populations in the area (Vieira, Borzone, Lorenzi, & de Carvalho, 2012).

William's Bay showed an overall decrease in the benthic macroinvertebrate population in terms of abundance, diversity and number of species upon disappearance of the *Thalassia testudinum* meadows from 2007 to 2016.

Table 10 shows a comparison of the species density and number of species among William's Bay and two sites in Florida (Stoner, 1980; Orth, 1973) and one site in Venezuela (Arana & Diaz, 2006).

Table 10
Comparison of macrobenthic species density and number of species between various sampling locations in Trinidad, Florida and Venezuela at different time periods

Country	Trinidad			Florida		Venezuela
Location	William's Bay			Apalachee Bay	Chesapeake Bay	Chacopata Beach
Year	2007 wet	2016 dry	2016 wet	1980	1973	2006
Species density (no. m ⁻²)	33373	16126	15797	8301	14284	4409*
No. of species	206	72	48	170	117	51*
* <i>Polychaetes only</i>						

The vegetated site in William's Bay, recorded in 2007 showed greater species density when compared to all other sites. The number of species recorded in William's Bay in 2007 was also greatest of all sites compared.

The percentage of carnivorous polychaetes in 2007 accounted for 14% of the number of species while deposit feeders accounted for 63%. In the *Thalassia testudinum* beds of Venezuela, carnivorous polychaetes were the most abundant accounting for 40% of all polychaete species (Arana & Diaz, 2006). Stoner (1980) reported 41% carnivorous and omnivorous polychaetes, 45% deposit feeders and 11% suspension feeders in Apalachee Bay Florida.

The species density recorded at William's Bay in 2007 can be considered very high as the other studies yielded square metre averages far below this number. Stoner (1980) reported a species density which is half the density of the unvegetated sites in 2016. *Zostera marina* beds in Chesapeake Bay (Orth, 1973) had a similarly lower number, and Arana & Díaz, (2006) reported a much smaller range of macrobenthos in Venezuela although this was for polychaetes only. When compared to the polychaete densities in William's Bay (Table 5), this number is still comparatively much lower. The number of polychaete species reported by Arana and Diaz (2006) is also lower than that recorded in 2007 wet season but greater than both of the 2016 sampling seasons (Table 5). Trinidad has a rich biodiversity that is reflected from its location close to the South American continent and proximity to the outflow of the Orinoco River Delta (Government of the Republic of Trinidad and Tobago, 2010). This has direct impacts on the marine biodiversity that is common to the nearshore benthic communities of the twin island state. It is possible the benthic macrofaunal biodiversity observed in William's Bay is a reflection of these factors.

Polychaete density in William's Bay for 2007 was found to be 17,354 polychaetes m². This number decreased to 7,579 ind. m² for the 2016 dry season and 8,530 ind /m² for the wet season. *Thalassia testudinum* beds in Venezuela recorded a monthly polychaete density ranging from 387 ind m⁻² (September) to 1 735 ind m⁻² in May, mean density = 989 ± 449 ind m⁻² (Arana and Diaz, 2006). The number of polychaete species described in 2007 (106) in William's Bay was far greater than the number of species found by Arana and Diaz (2006) who described a range of 21 to 51 species recorded in *Thalassia testudinum* beds from the Atlantic coast in Venezuela, with an average of 35.71 ± 10.71 species. The number of species recorded by Arana and Diaz (2006) in Venezuela was similar to that found in 2016 when *Thalassia testudinum* beds in William's Bay had been decimated. Differences were also reflected in polychaete populations between the sites. Polychaete abundance decreased overall.

The composition of the polychaete communities in William's Bay experienced notable change from vegetated to unvegetated habitat over this study period. *Lumbrineris januaris* (Grube, 1878) a carnivore, dominated the environment in 2007 and in 2016, *A. agilis*, a deposit feeder, was the dominant species. The data from 2007 showed the presence of carnivorous families such as Lumbrineridae, Nereididae and Orbiniidae. In 2016, opportunistic deposit feeding families such as Opheliidae, Paraonidae, Capitellidae and Spionidae were dominant, possibly due to an increase in organic load or a change in the availability of food, which favours these families (Sivadas, Ingole, & Nanajkar, 2010). In Apalachee Bay, Florida there was an abundance of carnivorous and suspension feeding species with increased seagrass biomass compared to increased abundance of deposit feeding and omnivorous species as seagrass biomass decreased (Stoner, 1980). Similarly, Arana and Diaz (2006) found tube building deposit feeders and carnivorous polychaetes to be dominant in *Thalassia testudinum* beds of Venezuela.

This study found a decrease in carnivorous, omnivorous and deposit feeding families from 2007 to 2016. The number of suspension feeding families remained the same (Table 3). Stoner (1980) postulated that increased carnivory associated with seagrass biomass can be due to the higher number of prey species such as protozoans, nematodes and other small organisms, and suggested that decreased deposit feeders at highly vegetated sites might be due to the presence of dense rhizome mats. This does not appear to be the case in William's Bay in 2007.

Ecosystem changes are also reflected by a change in the feeding habits of macrobenthos (Tilman et al., 1997) as such the loss of seagrass beds and the loss of smaller prey species would have prompted a response in the feeding habits of the polychaete communities. This was seen in the percentages of polychaete carnivores, omnivores, and deposit feeders, which varied between Trinidad communities and other communities studied. The Florida stations studied in Apalachee Bay had a gradient of macrophyte biomass ranging from 9 to 320 g dry wt m⁻², (Stoner, 1980). Macrophyte biomass recorded in William's Bay in 2007 fell within this range with a value of 191.0 ± 55.9 g dry wt m⁻². By 2016 this value decreased to 51.37 ± 52.7 g dry wt m⁻² in the dry season and eventually to 0 g dry wt m⁻² in the wet season

CONCLUSION

This study supports other studies conducted in Florida (Stoner, 1980) and Chesapeake Bay (Orth, 1973) that *Thalassia testudinum* beds support a higher abundance and diversity of benthic macroinfauna than unvegetated sites. This study is the first of its kind conducted on benthic macroinfaunal communities in the Caribbean. Data presented here show that loss of *Thalassia testudinum* meadows may have caused benthic macroinfaunal communities to decrease in abundance and diversity. Polychaete communities favour deposit-feeding genera while infaunal amphipods appeared to be less affected than their epifaunal counterparts. The study highlights the need for seagrass conservation and restoration to maintain biodiversity and support faunal food chains.

AUTHOR CONTRIBUTION STATEMENT

AK and RJ both contributed to conceptualisation, field sampling, processing and authorship of this study.

Declarations

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Figures

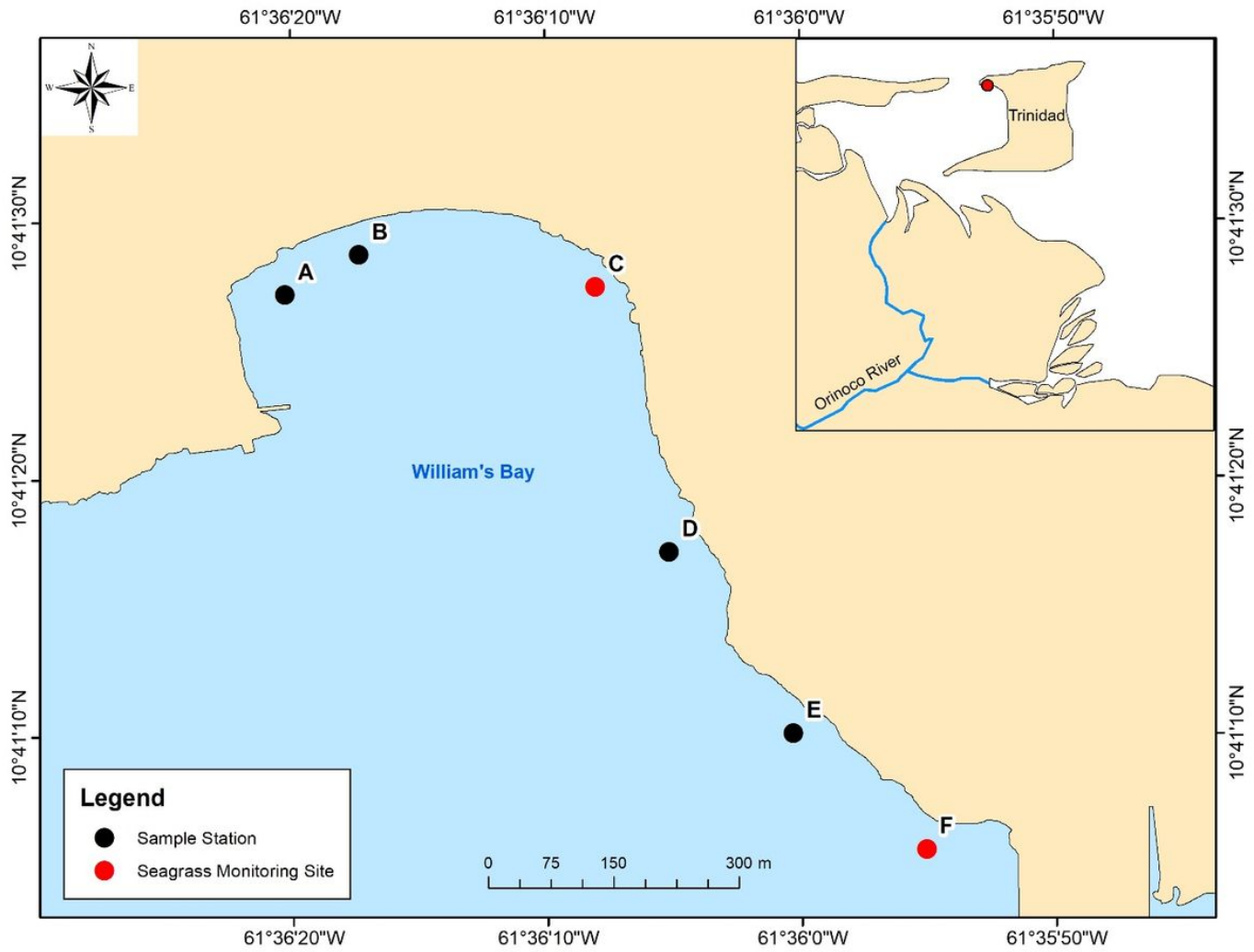


Figure 1

The location of William's Bay, Trinidad showing stations for seagrass monitoring and sediment sampling

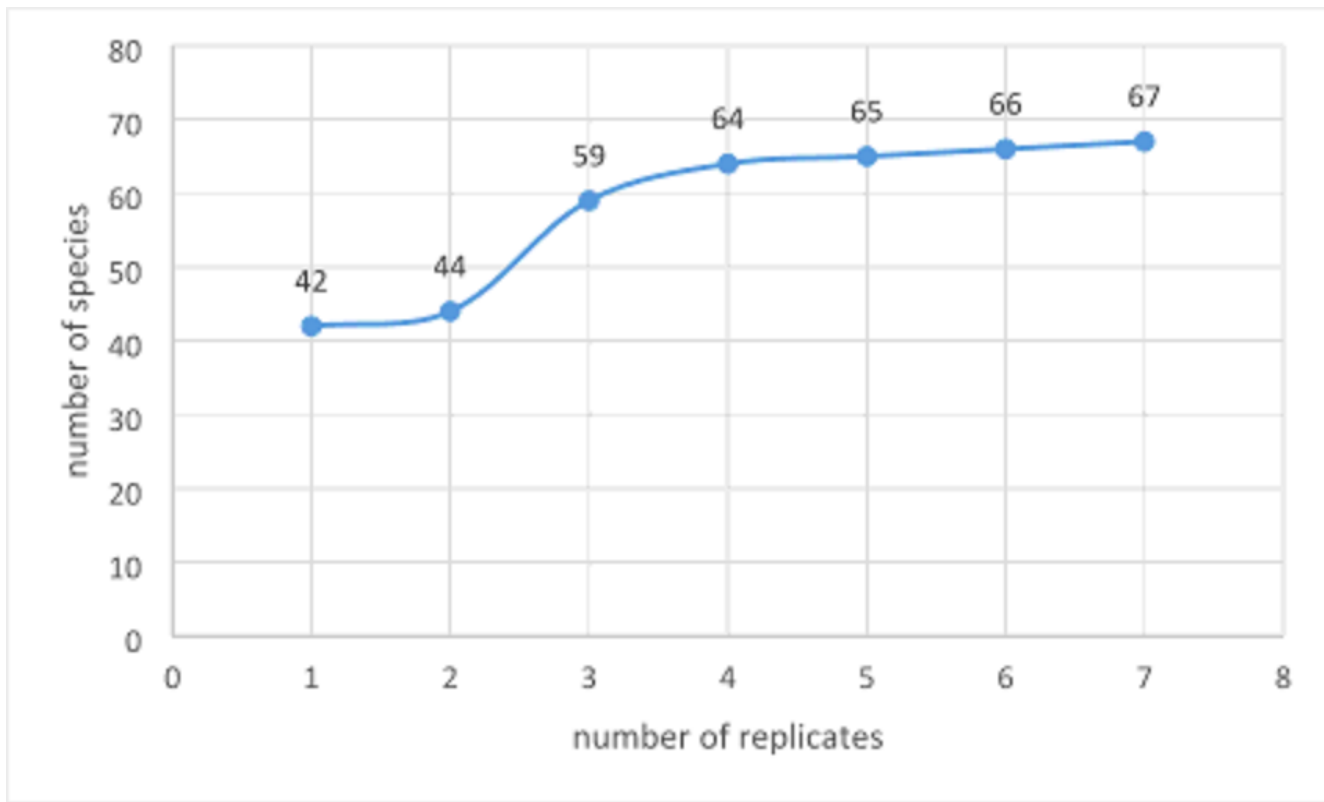
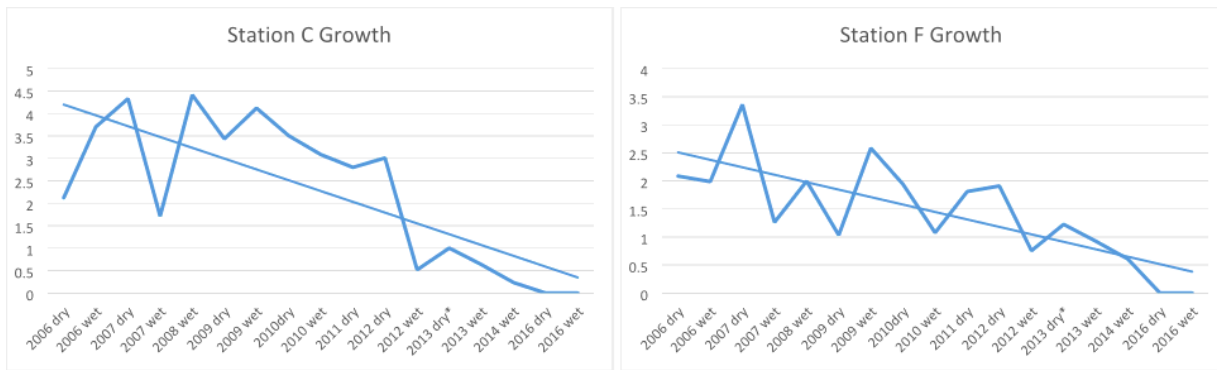
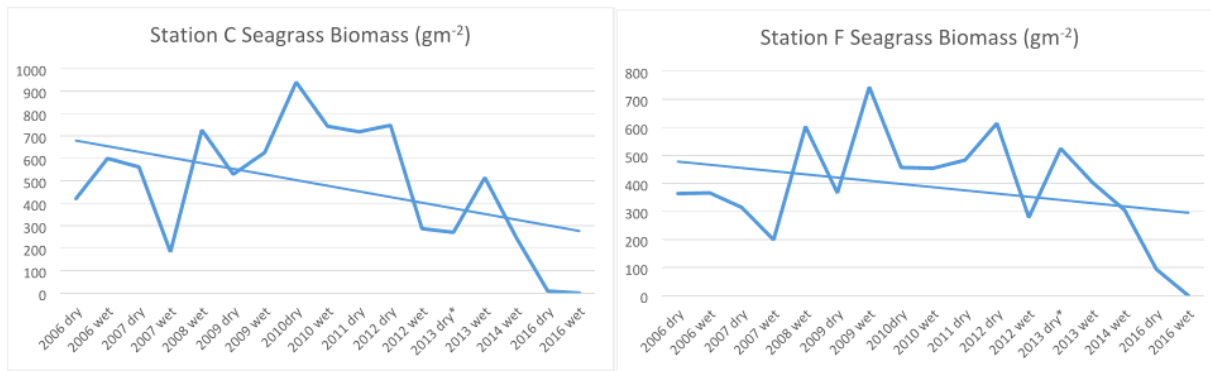


Figure 2

Cumulative frequency curve for pre-sampling experiment conducted at William's Bay



A



B

Figure 3

a Decline in seagrass aerial productivity for Stations C and F from 2006 to 2016

b Decline in total seagrass biomass for Stations C and F from 2006 to 2016



Figure 4
 Locations of sample sites in William's Bay and the control site in Bon Accord Lagoon