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research paper

Resampling 25 years later reveals fewer species but higher abundance of juvenile fishes in a Caribbean mangrove bay

[1] NOAA/NOS/NCCOS/MSE Biogeography Branch, 1305 East West Highway, Silver Spring, Maryland 20910

[2] CSS Inc., 10301 Democracy Lane, Fairfax, Virginia 22030

[3] NOAA/NMFS/SE Region Habitat Conservation Division, 3013 Estate Golden Rock, Christiansted, US Virgin Islands 00820

[4] Bonefish and Tarpon Trust, 2937 SW 27th Avenue, Suite 203, Miami, Florida 33133

[5] Florida Atlantic University Harbor Branch Oceanographic Institute, 5600 US-1, Fort Pierce, Florida 34946

[6] PO Box 3025, Kingshill, Virgin Islands 00851

* Corresponding author email: <matt.kendall@noaa.gov>, telephone: 240-533-0341

Matthew S Kendall [1] *
Bethany L Williams [2, 1]
Ashley Ruffo [3]
Arliss J Winship [2, 1]
Laughlin Siceloff [2, 1]
Aaron Adams [4, 5]
William Tobias [6]

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ABSTRACT.—The prop roots of mangroves play an important role as habitat for juvenile fishes. Revisit studies (>10 yrs apart) provide rare and valuable insights into the structure and stability of these systems in the face of escalating pressure from coastal development, climate change, and fisheries. We compared assemblages of juvenile fishes in the mangroves of a Caribbean estuary from 1991 to 1993 and 2018 to 2019 using trap collections to quantify changes and identify their potential drivers. Although the environmental and physical properties of the mangrove landscape were similar between the two periods, there were significant changes in many aspects of the fish assemblage. Compared to 25 yrs earlier, overall fish abundance (catch per unit effort, CPUE) was 3 to 7 times higher but overall biodiversity was 30% lower at the species level and 50% lower at the genus level. Taxa with dramatic changes in CPUE were mojarras (Gerreidae, 84% lower CPUE in 2018–2019), snappers (17 times higher CPUE), puffers (Tetraodontidae, 14 times higher CPUE), and moray eels (>200 times higher CPUE). Traps in 2019 also captured the first documented invasive Indo-Pacific swimming crab (*Charybdis helerii*) in the US Virgin Islands. The observed changes in the fish assemblage may be due to natural variations in recruitment, environmental influences, and/or hurricane disturbance, but for some species likely relate to declines in adult reef fish populations in the region.

Basic ecological understanding and management decisions for mangrove estuaries are best informed by examining how these habitats and their fish assemblages vary through time and the factors that can potentially influence them. Fish abundance, dominant species, and biodiversity are influenced by natural variations in recruitment, environmental setting, and disturbance regime. Concepts such as persistence and stability of fish assemblages necessarily require comparative data over long time intervals to be investigated (Connell and Sousa 1983, Castellanos-Galindo and Krumme 2014, Magurran et al. 2015). Despite their documented importance as habitat for juvenile fishes (Mumby et al. 2004, Manson et al. 2005, Adams et al. 2006, Dahlgren et al. 2006), mangrove systems have suffered from a historical bias toward research in developed countries, subtropical estuaries, and studies conducted for only short timescales (e.g., <2 yrs; Blaber 2002, Faunce and Serafy 2006). This lack of older data to place present day studies into context makes it important to utilize historical data where they exist (Smith et al. 2008, Ecoutin et al. 2010, Castellanos-Galindo and Krumme 2014).

Repeated snapshot assessments and long-term (>10-yr interval) monitoring studies on changes in fish fauna of mangroves are rare (Blaber 2002, Faunce and Serafy 2006). Ecoutin et al. (2010) examined a 10-yr interval in fish assemblages (1992–2002) in a mangrove system in West Africa. They linked reductions in biomass and trophic shifts to environmental degradation and overfishing. Castellanos-Galindo and Krumme (2014) examined a 13-yr interval (1999–2012) of fish data in 2 mangrove creeks in Brazil. In that tidally-influenced system (2–5 m range), composition of dominant species showed stability, but species richness and abundance declined by 38%–40%. Reduced recruitment due to environmental processes and nearby overfishing were postulated as potential drivers. Blaber et al. (2010) examined a 19-yr interval (1986–2005) of fish data in a mangrove estuary in northern Australia and found little change in diversity or catch rates. This was perhaps not surprising given the lack of commercial fishing and the stable local environment between the two time periods. Durdall (2018) examined a 21-yr interval (1995–2017) focused on juvenile fishes in a salt pond system (Great Pond) on St. Croix. Mangroves there experienced nearly complete turnover in fish assemblage composition due to severe drought-induced mortality and channel closure. Smith et al. (2008) examined changes after a 27-yr interval (1977–2004) in a riverine estuary in Puerto Rico. They found a major decline in overall species richness and abundance of mangrove fishes, especially for freshwater-adapted species at the head of the estuary, due to severe diversions of river water for municipal use.

Mangroves around the Caribbean island of St. Croix, US Virgin Islands offer another opportunity for a long-term perspective, but in a small island setting with little salinity fluctuation. Mangroves on St. Croix occur in only four main patches each with their own disturbance regime. These are Salt River Bay (18 ha of mangroves) and Altona Lagoon (19 ha) on the north side of the island, and Great Pond (16 ha) and Krause Lagoon (72 ha) on the south coast (NOAA Biogeography Program 2002). Salt River Bay and Altona Lagoon have been impacted by severe hurricanes and piecemeal upland development but have maintained channels open to the sea. In contrast, the tidal channel entering Great Pond experiences periodic shifts and blockage on a multidecadal scale due to sedimentation and storms (Lu et al. 1972), and in recent years, periodic clogging with drifting *Sargassum* (Langin 2018). Mangroves in Great Pond have lately experienced massive drought-induced mortality and loss of most fish fauna due to low water (Durdall 2018). Krause Lagoon was once the largest mangrove forest on St. Croix but was essentially destroyed in the 1960s for construction of a large commercial port and oil refinery (72 ha remain but primarily landlocked in an industrial complex; Tobias et al. 1996). The remaining mangrove forests around St. Croix may therefore be an especially important fish nursery for the island since it

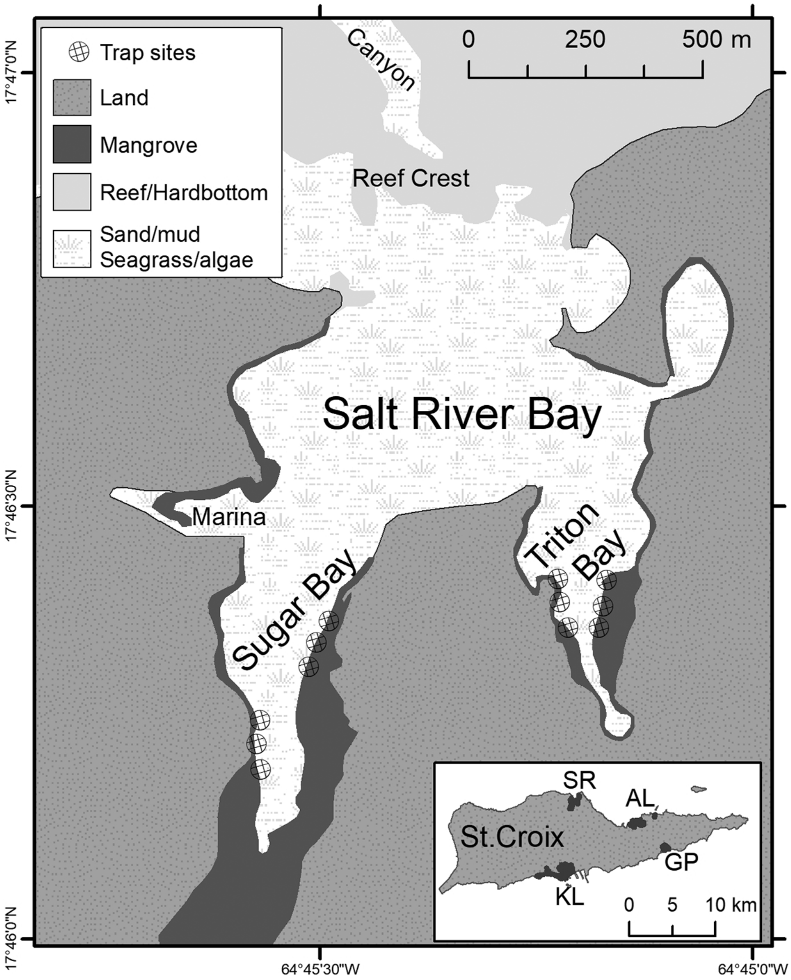


Figure 1. Salt River Bay study area showing habitats and trap positions in Sugar and Triton bays. Inset shows the location of Salt River Bay on St. Croix and the other mangrove areas around the island. SR = Salt River Bay, AL = Altona Lagoon, KL = Krause Lagoon, GP = Great Pond.

is relatively isolated from the rest of the Antilles on its own insular platform, separated from other islands by over 60 km and a 4000 m deep channel.

In the 1990s, researchers from the local management agency (Virgin Islands Department of Planning and Natural Resources, VIDPNR) recognized the need for an assessment of fish assemblages in the prop root fringe of the island's red mangroves (*Rhizophora mangle*) and conducted baseline studies (Tobias et al. 1996, Adams and Tobias 1999, Tobias 2001). Although many disturbance impacts had already taken place, these studies provide the earliest quantitative baseline of information available in these ecosystems.

In Salt River Bay, a National Historical Park and Ecological Preserve established in 1992, the fish assemblage in the mangrove prop root habitat of the area was sampled by VIDPNR monthly from March 1991 to April 1993 using fish traps and visual surveys (Fig. 1). Results were published initially as a government report (Tobias et al.

1996), and subsequently as a conference paper (Adams and Tobias 1999), using the same dataset. VIDPNR sought to quantify and compare the fish assemblage within two smaller bays in the Salt River Bay area. These bays, Triton and Sugar, were each divided into relatively unimpacted vs partially impacted shorelines based on levels of human development in the adjacent coastal zones. Unimpacted mangrove shorelines abutted forested hillside, whereas impacted shorelines were still lined by mangroves, but with somewhat lower density as forests transition to nearby roads or homes (Tobias et al. 1996, Kendall et al. 2005, NOAA Office for Coastal Management 2015). These bays also differ in the size of their surrounding watersheds. Sugar Bay is the outlet for the third largest watershed on St. Croix, draining an area over 1000 ha, whereas Triton Bay only drains a few ha of surrounding hillside (Oliver et al. 2011). Despite having the word "river" in its name, there is only an ephemeral stream flowing into the system. Furthermore, due to sea water flushing over the reef crest and a small tidal range, salinities are largely stable and similar to those offshore. Salinity throughout the bays is typically 35–38 (Tobias et al. 1996, Kendall et al. 2005). These conditions and development status remained consistent from 1991 to 2018.

A common challenge with historical records is the lack of metadata. This is especially true at institutions with only paper records of older studies, high staff turnover, obsolete (or nonexistent) data management plans, and limited capacity to archive records in secure settings. This can be compounded in many tropical areas which often lack fiscal resources for storage and have wet climates that are particularly unkind to paper records (Blaber 2002, Smith et al. 2008). Unfortunately, only publications with summary statistics remain from the original Salt River Bay study (Tobias et al. 1996, Adams and Tobias 1999), which limited the types of analyses that were possible. This can be somewhat mitigated by involving original authors, as was done here, to provide historical perspectives and fill in some missing metadata. Despite the challenge of working with older and incomplete records, it is important to take advantage of these valuable albeit imperfect data sets where they are available.

Twenty-five years after the 1991–1993 assessment, we reinvestigated the mangroves in Salt River Bay as habitat for juvenile fishes, following the trapping methods of the initial study to ensure comparability. Specifically, we sought to determine if changes had occurred in overall fish abundance, abundance of commonly caught species, seasonal peaks in dominant species, and overall biodiversity of fishes in trap samples from Triton and Sugar bays. The visual survey component of the original study was not repeated due to sand accretion at the formerly mangrove-fringed shorelines where those particular surveys took place. We then interpret the observed changes in the context of natural variations in recruitment, environmental influences, and changes in adult fish populations on nearby reefs.

Materials and Methods

Fish Sampling.—The fish assemblage of mangroves can be difficult to assess because turbidity inhibits visual techniques in many locations and the complex structure of the roots prevents nets or caisson sampling from penetrating much beyond the immediate fringe (Faunce and Serafy 2006). Although they provide an incomplete sample of fish assemblages, traps can provide an effective means to quantitatively sample fishes in this environment (Layman and Smith 2001). Trap samples are affected by trap type, mesh size, placement, and choice of bait, however, they can provide useful measures of the differences among sites or changes in a fish assemblage at the same sites if consistent designs are used at multiple locations and times (Adams and Tobias 1999, Layman and Smith 2001).

Methods used here necessarily mimicked those of Adams and Tobias (1999) for comparative purposes. Four sampling strata in the Salt River Bay ecosystem matched those used by Adams and Tobias (1999); two were in Sugar Bay and two in Triton Bay (Fig. 1). Site coordinates were initially identified by overlaying the original line illustration depicting sample locations (*see* figure 1 in Adams and Tobias 1999) onto present day satellite imagery. We navigated to those geographic coordinates in the field and then further modified them to reflect the 2018 position of the mangrove fringe. Once established, these new coordinates were used for trap sampling throughout the study.

Trap specifications were identical to those from Adams and Tobias (1999). Rectangular traps (92 × 57 × 19 cm) were constructed from 1.3 cm vinyl-coated wire mesh. The funnel opening was constructed at the small end of the trap using dimensions obtained from descriptions and photographs of the original traps. All traps in both time periods were baited with frozen herring which is commonly used as bait by local fishermen.

Traps were placed against the prop roots with the trap funnel facing parallel to the shoreline. In these bays, daily tidal fluctuations are small (about 30 cm) and traps remained completely submerged at low tide. Traps were deployed mid-morning and recovered approximately 24 hrs later. All sampling for a given month (i.e., one deployment per trap site) was conducted on consecutive days in both sampling periods. Adams and Tobias (1999) sampled monthly, however, evaluation of their results suggested that bimonthly sampling would be sufficient to detect taxon-specific seasonal patterns. We therefore reduced the frequency of sampling to bimonthly for a period of 1 yr (May 2018 to June 2019) to reduce effort but ensure that our temporal scope included an entire year. Similarly, trap position and spacing (50 m) was identical between the two sampling periods, however, the number of traps was reduced from 12 to 3 at each site to reduce sampling burden but still detect spatial differences. Lunar phase was not an influential variable in mangrove fish assemblages in nearby Puerto Rico (Rooker and Dennis 1991) and was not incorporated into the sampling design by Adams and Tobias (1999) or in the present study. All trapped fishes and crustaceans were identified to the lowest possible taxonomic level, measured (total length was only measured for the first 10 fish of each species per trap in the earlier period), and released at the point of capture. All original data from 2018 to 2019 have been archived for public access (Kendall et al. 2019).

Habitat Assessment.—The mangrove fringe immediately adjacent to each sample site was evaluated in 2019 to quantify habitat structure among strata. This was accomplished by measuring key variables known to affect fish assemblages (Laegdsgaard and Johnson 2001, Cocheret de la Morinière et al. 2004, Ellis and Bell 2004, Verweij et al. 2006). These included trap depth, percent cover of mangrove canopy above the trap based on upward facing digital photographs, number of prop roots penetrating the water surface within 0.75 m of the trap edge, combined percent cover of seagrass and algae within 1 m of the trap edge, root length underwater, and percent cover and thickness of epibionts on the 5 closest roots to the trap coordinates. Sediment at all sites consisted of mud and sand. Beginning in July 2018, temperature was recorded hourly at a site in each bay using automated data loggers. There are no quantitative data from the 1991–1993 sample period on any mangrove forest variables available for statistical comparison, although at the time of the study the eastern sides of Triton and Sugar bays were described as having "extensively covered mangrove shorelines" and the western sides as having "reduced mangrove cover" (Adams and Tobias 1999). No mention is made of any structural differences within each fringe of mangrove coast sampled in the original study (e.g., Sugar Bay – East) and standard error values were very narrow. No differences were readily apparent within those coastlines when reexamined at the time of the 2018–2019 period. This consistency within each stratum provided further rationale to reduce the number of samples.

Statistical Analysis.—Raw fish count data at the individual sample (trap) level from the original 1991–1993 study could not be recovered due to office damage from multiple hurricanes in St. Croix during the intervening years and lack of permanent electronic records. Therefore, the only data available for comparison were the summary values reported in Adams and Tobias (1999) and Tobias et al. (1996). This limited the types of statistical comparisons that could be conducted (Smith et al. 2008). Tabular data from these publications were copied into a new electronic database, and in some cases, numerical values were extracted for analysis by measuring axis intercepts from scanned figures.

Adams and Tobias (1999) caught 40 species from 19 families in fish traps from 1991 to 1993. Sugar Bay yielded five more species than Triton (33 vs 28) and the number of individuals and species richness in the catch were both significantly higher in the relatively more impacted western sides of the bays (Kruskal–Wallis tests, $P < 0.001$), although the absolute difference in values was low in these comparisons. Overall, 89% of the catch was comprised of fishes from only four families: Gerreidae (36%), Haemulidae (20%), Lutjanidae (19%), and Chaetodontidae (14%). Remaining families each comprised <2% of the catch. Size-frequency histograms of these commonly caught species indicate that catch was dominated by juveniles. Total abundance by fish family was available in tabular data and plotted on a log scale by Adams and Tobias (1999).

To standardize data for comparisons, we converted total catch values to catch per unit effort (CPUE) in each sampling period by dividing total catch by the number of traps set. Values were plotted on a $\log_2$ scale to better visualize differences in the range of CPUE values. Note that this approach is useful for comparing the relative abundance of common fishes assuming equal effort, but is not appropriate for examining relative biodiversity, a topic best investigated through rarefaction as described below (Heck et al. 1975, Gotelli and Colwell 2001).

Number of species caught per trap, fish abundance per trap, and mean fish size for abundant species were compared between time periods and locations using *t*-tests (e.g., was catch different in Triton East in 1991–1993 than in Triton East in 2018–2019?). Welch's modified *t* statistic was used to account for unequal variance and different sample sizes between the two time periods (Zar 1999).

Considering just the 2018–2019 data, differences in abundance per trap among the four bay/coast combinations were analyzed with Kruskal–Wallis tests. This was due to the heterogeneous dispersion of the data among locations and also because this was the same test used in the original study period and it was informative to use a test with the same sensitivity. If significant overall, Wilcoxon pairwise tests that are protected for multiple comparisons were performed (e.g., Triton West vs Sugar West). Differences in number of species caught per trap among the four bay/coast combinations were analyzed with ANOVA (bay, coast, and interactions) since parametric assumptions were met, but also with Kruskal–Wallis rank-based analysis to match the test and sensitivity used to detect patterns in the original study. Raw data from individual traps were not available for 1991–1993 which limited some types of statistical comparisons. Due to the small sample size (n = 3 per bay/coast combination), mangrove variables (e.g., canopy cover) from the 2018–2019 sampling period were also evaluated with Kruskal–Wallis tests to determine if there was a difference among any locations followed by Wilcoxon pairwise comparisons to determine which pairs were significantly different (e.g., Triton West vs Sugar West).

Some seasonal and interannual comparisons were also possible between the two sampling periods. Seasonal patterns in catch were available for the most commonly caught species from the 1991–1993 data: schoolmaster snapper, French grunt, and yellowtail snapper (Tobias et al. 1996). Data for yellowfin mojarra, another commonly caught species in 1991–1993, were also available, however, none of that species was caught in 2018–2019. Mean monthly abundance values were measured from figure 10 in Tobias et al. (1996). Unfortunately, estimates of variability such as standard error were not available for these data. For comparison purposes, the mean monthly catch was expressed as a proportion of the month with the highest catch in Tobias et al. (1996). The two complete years 1991 and 1992 were plotted as separate lines on a monthly basis. In the 2018–2019 samples, catch for each of these three species was averaged among all traps by month. As with the 1991–1993 data, mean monthly catch was expressed as a percentage of the month with the highest catch from the 2018–2019 sampling period and plotted for comparison. This enabled us to compare not only the timing of peak abundance but also the relative magnitude of seasonal catch within each study.

To determine if the number of species differed between the two sampling periods we used rarefaction curves (Heck et al. 1975, Gotelli and Colwell 2001). Rarefaction corrects for different levels of sampling effort when comparing species richness between two or more studies. Tobias et al. (1996) used a larger number of traps per site [12 by Tobias et al. (1996) vs 3 in this study], increased frequency of sampling (monthly vs bimonthly), and conducted their study for a longer duration (2.5 vs 1.1 yrs) compared to this study [total of n = 1176 individual trap samples by Tobias et al. (1996) vs n = 84 in this study]. This much-reduced trapping effort of the recent sampling provided less opportunity to catch individuals and species, and prevented direct comparisons of total species richness between the two time periods. Rarefaction curves use the catch data to calculate the expected number of species caught as sampling effort increases (Heck et al. 1975, Gotelli and Colwell 2001). The statistical equation is based on the principle that as larger samples are drawn, the chance of sampling more species increases. Once computed, the expected number of species can be compared between time periods for any given number of samples or individuals collected. Species- and genus-richness curves for each sampling period were generated on a per individual caught basis using the iNEXT package in R (Hsieh et al. 2016). Richness values include 95% confidence intervals, and for the 2018–2019 data, extrapolated predictions of richness to facilitate comparison with 1991–1993 but only up to twice the number of actual individuals sampled as advised by Chao et al. (2014).

Table 1. Mean (SE) of mangrove habitat variables from each location (e.g., Triton-East) as well as the *P*-value from the Krusal–Wallis test for differences among locations.

Habitat variable	Triton-East	Triton-West	Sugar-East	Sugar-West	*P*-value
Depth (cm)	60 (4)	114 (39)	81 (6)	61 (3)	0.07
Seagrass/algae % cover	83 (12)	48 (13)	83 (9)	88 (7)	0.19
Mangrove canopy % cover	47 (9)	90 (8)	52 (25)	85 (5)	0.14
Number of prop roots	13 (3)	8 (1)	14 (4)	7 (1)	0.08
Epibiotic % cover	69 (2)	89 (4)	76 (9)	72 (7)	0.23
Epibiotic thickness (cm)	11 (2)	17 (3)	17 (3)	12 (4)	0.46
Submerged root length (cm)	40 (6)	36 (6)	52 (10)	39 (7)	0.58

Results

There were no significant differences among trap locations in any of the seven characteristics of the mangrove habitat that were measured in 2019 (Table 1). These results must be interpreted cautiously, however, due to the low sample size (n = 3) and irregular variance in some variables. Trap depth (mean = 79 cm among all 12 sites), seagrass/algae cover around the traps (mean = 76%), mangrove canopy cover (mean = 68%), number of nearby prop roots (mean = 11 roots), and length of submerged segments of prop roots (mean = 41 cm) were similar at all bay and coast combinations. Epibiotic flora and fauna colonizing the submerged portions of prop roots were dominated by various types of macroalgae (turf, fleshy, filamentous, etc.; mean = 69% cover on individual roots). Barnacles were present on 50% of the roots but always in low abundance (mean = 3.7% cover). Oysters were present on 22% of the roots and occurred with low percent cover (1%–4%), however at one site on the western side of Triton Bay, oysters reached 35%–50% cover on all five roots evaluated. Sponges were present on 15% of roots with highly variable percent cover ranging from 1% to 92% on individual roots. Other types of epifauna occurred more rarely such as feather duster worms (present on 2 roots), tunicates (2 roots), and anemones (1 root). There were however, no significant differences in percentage of overall epibiotic cover on prop roots among bays or sides of the bays (mean = 77%) and no difference in maximum thickness of epibiotic cover among sites (mean = 14 cm).

Temperature was recorded hourly in each bay beginning in July 2018 but unfortunately, sensors in both data loggers failed after only a few months. Data collected prior to sensor failure revealed an average water temperature of 30.9 °C in both bays in August, which is typically the warmest month in this area (Kendall et al. 2005). Average monthly temperature declined in both bays steadily to 26 °C in January before sensors failed. The daily temperature range was about 2–3 °C in Sugar and about 1–2 °C in Triton with lowest temperatures around 6:00 and highest around 16:00. Two rain events in September (1.1 in on 31 August, and 1.7 in on 15 September; National Centers for Environmental Information) resulted in lower water temperatures in both bays (by approximately 2 °C compared to average conditions that month) for a period of 3–4 d.

Nearly all individuals in both time periods can be considered juvenile reef fishes based on size at maturity studies (Froese and Pauly 2019). CPUE plotted by family revealed some similarities between the two time periods (Fig. 2, Online Appendix A). Catch rate of grunts (Haemulidae), parrotfishes (formerly Scaridae, now subfamily

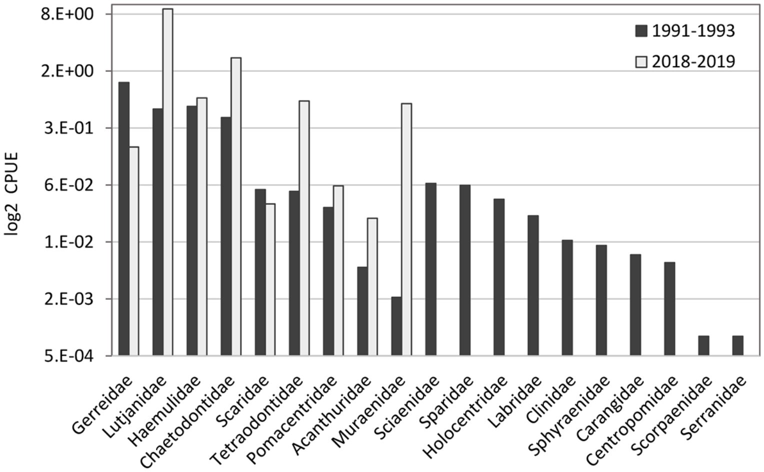


Figure 2. Catch per unit effort (CPUE) by fish family sampled in 1991–1993 (black) and 2018–2019 (grey). The *x*-axis is ordered by taxa caught in both time periods followed by those caught in only one time period. Note $\log_2$ CPUE scale.

Scarinae), and damselfishes (Pomacentridae) was similar in the two periods. A few taxa were consistently among the most abundant including snappers (Lutjanidae), grunts, and butterflyfishes (Chaetodontidae). There were also some large differences in abundance of those taxa common to both sampling periods. Those with dramatic changes were mojarras (Gerreidae, 84% lower CPUE in 2018–2019), snappers (17 times higher CPUE in 2018–2019), puffers (Tetraodontidae; 14 times higher CPUE), and moray eels (>200 times higher CPUE). Also of note, there were no new fish families in the 2018–2019 catch that were not present in 1991–1993. Conversely, ten of the fish families present in the 1991–1993 catch were absent in 2018–2019. However, changes in biodiversity are better evaluated in the rarefaction analysis which accounts for differences in sampling effort for rare taxa.

The number of fishes caught per trap was significantly higher in 2018–2019 than in 1991–1993 for all bay/shoreline combinations (Table 2). Average number of fishes caught per trap in 1991–1993 was 2.6 to 3.8 in all bay/shoreline combinations. In contrast, average number of fishes per trap in 2018–2019 was about 3 to 7 times higher. Also of note, the western sides of both bays had higher abundance than the eastern sides in both sampling periods (*see* Online Appendix B for most abundant species by location). Considering just the 2018–2019 data, there was a significant effect of

Table 2. Average fish abundance (SE) per trap compared between 1991–1993 and 2018–2019 using Welch's *t*-test. Values from 1991–1993 are from table 2 in Adams and Tobias (1999). Letters next to 2018–2019 data denote locations with significantly different means within the sampling period using the Kruskal–Wallis test.

Site	1991–1993		2018–2019		Welch's *t*-test			
	Mean	SE	Mean	SE	SE pooled	*t*	df	*P*
Triton-East	2.55	0.24	9.4^{a}	1.64	1.66	4.1	20	<0.001
Triton-West	3.27	0.23	12.2^{a}	1.73	1.75	5.1	20	<0.001
Sugar-East	2.90	0.23	8.2^{a}	0.98	1.01	5.3	22	<0.001
Sugar-West	3.76	0.32	23.4^{b}	3.49	3.50	5.6	20	<0.001

Table 3. Average number of fish species (SE) per trap compared between 1991–1993 and 2018–2019 using Welch's *t*-test. Values from 1991–1993 are from table 2 in Adams and Tobias (1999). There were no locations with significantly different means within the 2018–2019 data using the Kruskal–Wallis test.

Site	1991–1993		2018–2019		Welch's *t*-test			
	Mean	SE	Mean	SE	SE pooled	*t*	df	*P*
Triton-East	1.14	0.06	3.0	0.36	0.36	5.09	21	<0.001
Triton-West	1.55	0.08	3.6	0.25	0.26	7.81	24	<0.001
Sugar-East	1.32	0.07	2.6	0.25	0.26	4.93	23	<0.001
Sugar-West	1.65	0.08	3.2	0.17	0.19	8.24	30	<0.001

location (Kruskal–Wallis test, df = 3, $\chi^2 = 13.6$, $P < 0.0013$). Pairwise comparisons among locations in that period revealed that there were no differences in fish abundance among locations except for Sugar West (SW) which was significantly higher than all other locations (Wilcoxon pairwise comparison: SW vs TE, $P = 0.003$; SW vs TW, $P = 0.02$; SW vs SE, $P < 0.0004$; Online Appendix B).

The number of species caught per trap was also significantly higher in 2018–2019 than in 1991–1993. Average number of species caught per trap in 1991–1993 was 1.1 to 1.7 in all bay/shoreline combinations (Table 3). In contrast, average number of species caught per trap in 2018–2019 was over twice as high at 2.7 to 3.6. Considering just the 2018–2019 data, there were no significant effects of any aspect of location on species caught per trap whether analyzed parametrically with ANOVA (df = 3, $F = 2.04$, $P = 0.11$) or nonparametrically with Kruskal–Wallis (df = 3, $\chi^2 = 6.2$, $P = 0.1$) as was done in 1991–1993.

Species richness of the mangrove fishes in this system appears to have declined in the past 25 yrs (Fig. 3A). Rarefaction results suggest that when similar numbers of individuals were sampled between the two time periods, species richness was about 30% lower in 2018–2019 compared to 1991–1993. For example, rarefaction predicted that when 1000 individuals were sampled in 1991–1993, about 30 species would be present, whereas in 2018–2019 when the same number of fishes were encountered,

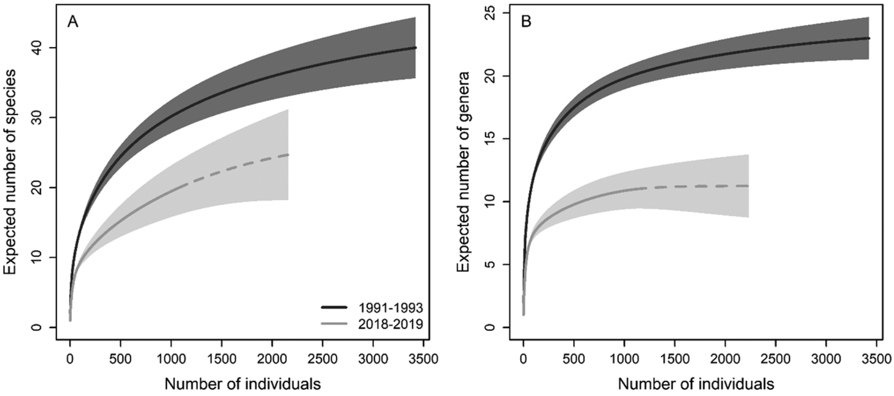
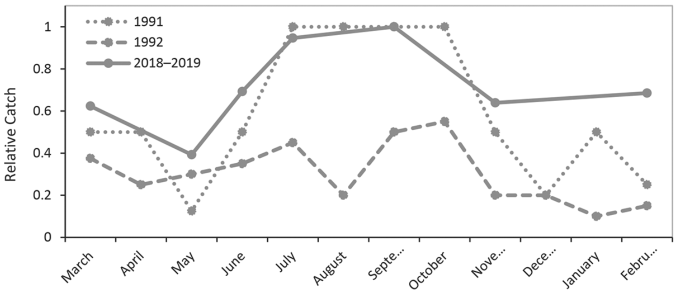
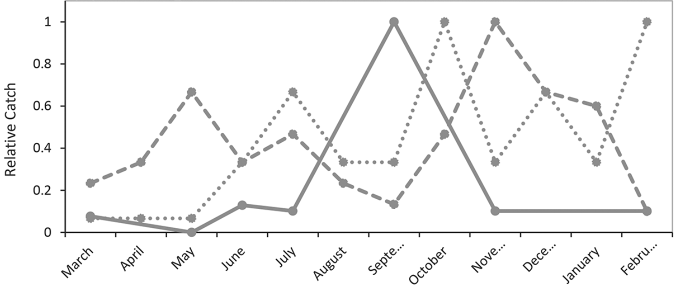


Figure 3. Expected number (standard error) of (A) species and (B) genera encountered based on the number of individuals sampled in 1991–1993 (black) and 2018–2019 (grey). Rarefaction predictions depicted by solid lines extend from 1 to the total number of fishes sampled in each period. Dashed line represents extrapolated richness for 2018–2019. Shaded areas denote 95% confidence intervals.

(A) schoolmaster snapper



(B) French grunt



(C) yellowtail snapper

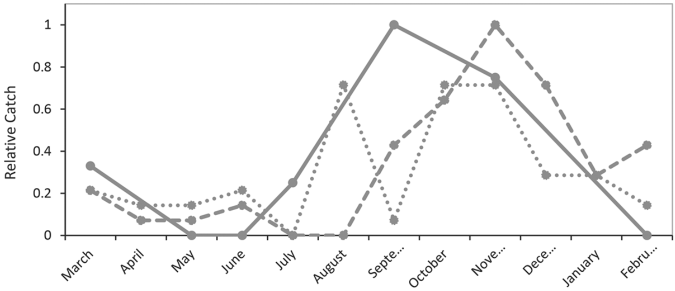


Figure 4. Catch by month for (A) schoolmaster snapper (*Lutjanus apodus*), (B) French grunt (*Haemulon flavolineatum*), and (C) yellowtail snapper (*Ocyurus chrysurus*). To enable comparison, values are expressed as percentages relative to the month with the highest catch within each study and then plotted by month.

only 19 species were present. Predicted species richness did not reach an asymptote in either period, suggesting that more species would be encountered given greater sampling effort, but the approximately 30% difference persists. The outcome is similar when considered at the genus taxonomic level. The number of genera present in 2018–2019 was only 50% of those present at the same level of sampling effort in 1991–1993 (Fig. 3B). Unlike the results at the species level, both periods appeared to be closer to their maximum (i.e., asymptotic) values of expected genera richness given the sampling effort.

Seasonal peaks in abundance were apparent for some of the most commonly caught species despite variations in magnitude on an interannual basis (from Tobias et al. 1996). Although the magnitude of the peaks varied between the two sampling periods, their seasonal timing was consistent for all 3 species considered (Fig. 4).

Table 4. Average fish length (TL, mm) for three fish species compared between 1991–1993 and 2018–2019. Values for 1991–1993 are from table 3 in Adams and Tobias (1999).

Site	1991–1993			2018–2019			Welch's *t*-test			
	Mean	SE	*n*	Mean	SE	*n*	SE pooled	*t*	df	*P*
French grunt	79.7	0.72	623	80.1	1.89	59	2.02	−0.17	76	NS
Schoolmaster	97.7	1.73	409	91.3	1.00	647	2.00	3.21	679	<0.002
Yellowtail snapper	94.3	2.32	173	100	3.26	28	4.00	−1.44	59	NS

Peak catch for schoolmaster snapper occurred July–October in 1991, 1992, and 2018–2019 (Fig. 4A). Peak catch in 1992 occurred at the same season in 1991, but was 50% lower in magnitude and more variable. For French grunts, peak catch occurred in fall months but in discrete events in September (2018–2019), October (1991), or November (1992) depending on the year with an additional pulse in February 1991 (Fig. 4B). Peak catch was of a similar magnitude in 1991 and 1992. For yellowtail snapper, peak catch was consistently in summer/fall in all years from August to December (Fig. 4C). Peak catch was of a similar magnitude in 1991 and 1992.

Mean fish size was not significantly different between the two sampling periods for French grunts or yellowtail snappers (NS Welch's *t*-test; Table 4). There was a significant difference in mean size of schoolmaster snapper, although the actual difference in mean size was small and statistical power was high due to large sample sizes. In 1991–1993 mean length was 97 mm whereas in 2018–2019 it was 91 mm (Welch's $t = 3.21$, df = 647, $P < 0.002$).

Crustaceans were caught but not recorded in 1991–1993 (Adams and Tobias, pers comm) and were a highly abundant component of the catch in 2018–2019. Crabs from the genus *Callinectes* were present in 79% of all trap samples and were the most abundant part of the catch in 26% of traps. Also of importance, the first records in the Virgin Islands of the invasive Indo-Pacific swimming crab *Charybdis hellerii* (A. Milne Edwards, 1867) were observed in this study (Mantelatto and Garcia 2001, Ferry et al. 2017).

Discussion

We compared assemblages of juvenile fishes in the mangroves of a Caribbean bay from the 1991–1993 and 2018–2019 sampling periods using trap collections. Although the environmental and physical properties of the mangrove landscape were similar between the two periods, there were significant changes in many aspects of the fish assemblage. These changes may relate best to population trends on nearby reefs.

Overall Patterns and Potential Causes.—Compared to 25 YA, assemblages are still comprised almost entirely of juvenile reef fishes, but there have been several changes to the fish assemblage in the mangroves of Salt River Bay. There appear to be more schoolmaster snappers and moray eels, but fewer mojarras. Mojarras (*Eucinostomus jonesii* and *Gerres cinereus*) were the numerically dominant fishes in the traps 25 YA (Tobias et al. 1996) and are a principal target of the shore-based fishery around St. Croix (Goedeke et al. 2016). This decline in juvenile mojarras is consistent with expectations given the severe decline in adults documented by a reef-monitoring program (2001–2012) for northeastern St. Croix (Jeffrey et al. 2019).

Diver surveys observed *G. cinereus* on 27% of reef surveys in 2001 but only 2% in 2012, a severe and significant linear decline (df = 11, $R^2 = 0.63$, $P < 0.002$). Some studies take the approach of examining adult fishes on reefs for the possible influence from nearby mangroves (e.g., Mumby et al. 2004, Serafy et al. 2015, Shideler et al. 2017), but this relationship is of course part of an ontogenetic cycle. We instead examined juvenile fishes in mangroves and found evidence of possible influence of adult populations from nearby reefs.

Some species showed an increase in abundance. Another fishery species, schoolmaster snapper, was commonly caught in both sampling periods, but its abundance in the 2018–2019 traps increased dramatically (17 times higher) compared to the 1991–1993 period. This species, however, showed no significant trend in adult abundance on reefs in northeastern St. Croix (Jeffrey et al. 2019), suggesting another influence than a spawner-recruit relationship such as reduced juvenile mortality. Also of note in the 2018–2019 samples, moray eels were not only more abundant than 25 YA but were by far the largest component of the catch in terms of individual biomass. Mean eel length or weight in the 2018–2019 samples was 76 cm or 927 g and always vastly outweighed the rest of the catch when present (Bohnsack and Harper 1988).

At the assemblage level, it is especially troubling that fish richness was 30% (species) to 50% (genus) lower than it was 25 YA although the environment was consistent. Many studies have examined the differences in fish diversity among various mangrove areas (Blaber 2007), but only a few have compared biodiversity in the same mangrove estuary over multiple decades. A recent study on mangrove fishes at Great Pond, St. Croix documented a 78% decline in species richness of native fishes, however, that is not surprising given that the site has undergone profound hydrological changes including blockage of the ocean channel, mangrove die-off, and complete drying (Durdall 2018). Similarly, at a riverine, mangrove-lined estuary in Puerto Rico over 27 yrs (1977 and 2004), fish species richness declined by 48% (Smith et al. 2008). This was attributed to increased diversions of fresh-water for municipal use and indeed most of the decline in species richness was for freshwater adapted fishes. Although conducted over shorter timescales (10–12 yrs), fish assemblages in other mangrove systems with documented reductions in species richness have implicated environmental influences as well as overfishing as potential causes (Ecoutin et al. 2010, Castellanos-Galindo and Krumme 2014). In contrast to these studies, the fish fauna of a mangrove estuary in northern Australia showed little change in catch rate or diversity over a 19-yr interval (Blaber et al. 2010). That stability was attributed to the lack of any notable environmental change and ongoing prohibition of commercial fishing in the area.

The documented 30%–50% decline in fish biodiversity in a mangrove system so physically similar to its condition 25 YA is suggestive of potentially serious underlying problems. Monitoring in a nearby marine protected area (MPA; Buck Island Reef National Monument, northeastern St. Croix) showed a drop of 10% in species richness of reef fishes on visual transects between 2003 and 2010 (Pittman et al. 2014), which if linearly extrapolated to 25 yrs reaches a comparable decline of 35%. Areas outside that MPA showed no decline although richness values outside the MPA were lower to begin with (Pittman et al. 2014) due to earlier declines. In fact, a study of reef fishes at a site off western St. Croix conducted from 1994 to 1996 revealed a 35% decline in species richness (Adams 2001) and St. Croix in general has been described as severely overfished (Kadison et al. 2017). Causes for this region-wide decline in reef fishes are long-standing, well-documented, and include interacting effects such as pervasive overfishing, habitat degradation, and climate change (Hughes 1994, Jackson 1997, Hawkins and Roberts 2004). It is concerning that these effects demonstrated for adults on the reef may be translating into severe reductions of juvenile diversity in mangroves. Even if mangrove habitats are structurally intact, they are not receiving the diversity of recruits that they once were. Protecting them will do little to replace the lost biodiversity on adjacent reefs unless improvements are made there as well (Mumby et al. 2004, Manson et al. 2005, Serafy et al. 2015).

It should be noted that the rarefaction analysis in this study was conducted on a per individual basis because trap-level data were not available from the earlier study. For patchy distributions, individual-based rarefaction tends to overestimate the number of genera that would have been found with less effort (Gotelli and Colwell 2001). This was less of a concern in our study because we were more interested in the relative differences in biodiversity between the two time periods rather than precise estimates of species richness per se. It may seem counterintuitive that overall richness was lower based on rarefaction analysis but average per-trap richness was higher in the recent sampling period. This is due to the high abundance of one or two species in the traps, which when added to the rarefaction curves, do not add richness. Furthermore, it is known that traps under-sample transients and large fishes (Layman and Smith 2001, Rooker and Dennis 1991). However, because such biases are consistent for both time periods due to uniform trap specifications, it is suspected that the differences in the two time periods are due to real differences in the fish assemblages.

There are several possible influences on the differences observed between sampling periods. An obvious suspect is natural variation in supply and/or settlement rates, as was suggested for an altered mangrove assemblage in Brazil (Castellanos-Galindo and Krumme 2014). Interannual differences in recruitment can be influenced by multiple factors such as variable fecundity and size of spawning populations, variable survivorship of larvae during the pelagic stage, and irregular settlement success due to ocean currents (Caselle and Warner 1996, Hamilton et al. 2006, Chérubin and Garavelli 2016). However, it should be noted that in empirical studies of recruitment variability around St. Croix, Salt River experienced no significant difference in interannual recruitment (bluehead wrasses, *Thallasoma bifasciatum*, and other species) unlike sites on the northwest and southeast coasts of the island (Caselle and Warner 1996). Recruitment can indeed vary among years at individual sites, but the dominant and consistent pattern on St. Croix is for increasing settlement westward along the north shore, with Salt River being positioned centrally and experiencing less interannual variation than elsewhere around the island (Hamilton et al. 2006).

It should also be emphasized that most fishes in the size classes that are caught in the mangroves by the mesh size of these traps are later stage juveniles. For example, most of the French grunts in the catch were 60–80 mm TL, which places them in the medium or large juvenile size classes and 50–150 d post settlement (Shulman and Ogden 1987). For fishes at this stage, sensitivity analysis revealed that mortality rate is 100 times more important than settlement rate in determining abundance (Shulman and Ogden 1987, Watson et al. 2002). It is estimated that <1% of initial recruits survive to reach the approximately 70 mm TL size class captured in the mangrove fringe. Another empirical study on St. Croix documented that larval mortality is strongly density dependent, especially during the first day after settlement, and smooths out recruitment peaks into more consistent levels of juvenile density

(Caselle 1999). Thus, mortality dampens the influence of recruitment variation by the time fishes reach the trappable stage in the mangroves at Salt River Bay.

Hurricanes are a regular occurrence in this part of the Caribbean and are a potential source of variation between the two time periods. Hurricane Hugo passed over St. Croix on September 18, 1989 as a Category 4 storm. Similarly, Hurricane Maria passed by the island on September 19, 2017 as a Category 5 storm. Therefore, sampling in these two studies was conducted at a coincidentally comparable 11–30 mo after Hugo (Tobias et al. 1996) and 6–21 mo after Maria (this study). Both storms severely impacted the mangroves of Salt River Bay. Damage was especially severe on western shores of Triton and Sugar bays during Maria (pers obs) and the southern end of Sugar Bay's old-growth mangroves during Hugo (Kendall et al. 2005). Also of note, Adams and Tobias (1999) described the eastern shores of both bays during their sampling as "extensively covered mangrove shorelines", and the western sides as having "reduced mangrove cover", a condition consistent with post Maria observations. Although there certainly were uneven impacts and Hugo was more devastating due to its slower passage over the island, the coincidental similarity in strength of the storms, their seasonal timing, the overlap in poststorm sampling periods, and overall resilience of small fish assemblages to storms (Adams and Ebersole 2004) suggests that both sampling periods experienced similar hurricane disturbance and recovery timelines.

Trap studies may be impacted by interspecific interactions as fishes approach the traps or within the traps themselves. For example, the higher abundance of juvenile fishes in the 2018–2019 traps could have attracted the higher abundance of moray eels compared to the earlier study. On the other hand, the presence of the eels in many traps may also have resulted in trap avoidance by prey species. Similarly, there is evidence of exclusion or avoidance interactions among juveniles of other species that may have affected catch. Damselfishes (Pomacentridae) are territorial and can aggressively exclude surgeonfishes (Acanthuridae) as food competitors as well as butterflyfishes (Chaetodontidae) as potential egg predators (Shulman et al. 1983). The presence of larger and earlier settling snappers (Lutjanidae) can similarly reduce the numbers of young grunts (Haemulidae; Shulman et al. 1983).

Spatial Patterns.—Differences in fish assemblages between Triton and Sugar bays did not match expectations based on watershed differences. Fish assemblages often differ among mangroves based on factors such as forest characteristics, hydrology, and landscape setting (Blaber 2007, Dorenbosch et al. 2007, Pittman et al. 2007, Drew and Eggleston 2008, Martin et al. 2015). Both Sugar and Triton bays are approximately the same distance to other downstream habitat types such as seagrass beds, coral reefs, and a shared channel at the head of a submarine canyon (Fig. 1; Kendall et al. 2005). However, their upstream landscapes are quite different. Sugar Bay is the outflow point of the third largest watershed on St. Croix (about 1500 ha) whereas Triton Bay's watershed is only approximately 100 ha (Oliver et al. 2011). Land-use patterns in these watersheds are also quite different, with Triton Bay's small watershed being dominated by continuous forest/scrub and Sugar Bay receiving runoff from a mixed-use mosaic of small farms, forests, residential housing, roads, and small commercial properties (NOAA Office for Coastal Management 2015). Human land-use in this watershed has been correlated with reduced health of nearby reefs (Oliver et al. 2011). Turbidity, salinity, and dissolved oxygen are generally similar in Triton and Sugar bays (Kendall et al. 2005) except during rain events. Rain in the larger watershed of Sugar Bay regularly results in a turbidity plume that can be observed moving northward along the western side of the estuary and then flowing westward past the fringing reef with the prevailing currents (Kendall et al. 2005). Based on this, it was anticipated that there would have been more differences in the juvenile fish assemblages between the two bays, however that was not reflected in the results.

Local properties of the mangroves at sample sites can also influence fish assemblages (Laegdsgaard and Johnson 2001, Cocheret de la Morinière et al. 2004, Ellis and Bell 2004). There were, however, few differences observed between the bays. Temperature was similar between the two bays and there were no significant differences in habitat variables at trap sites including mangrove canopy, number of prop roots, depth, epibiotic colonization on roots, and underlying seagrass/algae coverage.

Although there were few differences between the bays overall, there was a difference in fish abundance per trap with higher values at Sugar West than at other sites in 2018–2019. Fish abundance and species richness were both significantly higher at western sites than eastern sites in both bays in data from the 1991–1993 sampling period. Adams and Tobias (1999) hypothesized that the pattern was due to lower natural habitat availability and therefore trap attraction on the western sites at the time of their study. They describe the western sites as being "partially impacted by development" which consists of a road and a few houses, a status unchanged in 25 yrs. However, no quantitative differences in the mangrove variables were found in 2018–2019, yet the difference in fish abundance persisted for Sugar West. This suggests other processes as the cause of these differences. Factors to investigate include solar illumination, which differs on the bay sides as clouds typically increase during the day, and/or wind forcing since the westward trade winds dominate at this latitude (Kendall et al. 2005). Transport of mangrove detritus, wind-driven circulation of particulate food sources, or algal differences may provide an enhanced energy base for fish assemblages on the western sides of the bays.

Seasonal Patterns.—Data for only four species were available for seasonal comparisons based upon figures in Tobias et al. (1996), and only three of those were caught in sufficient abundance to enable comparisons between studies. Seasonal peaks were evident in both time periods and were discernable with monthly sampling (Adams and Tobias 1999) as well as the less labor intensive bimonthly sampling used in the present study. Peak catch of French grunts occurred in a bimodal pattern in the 1991–1993 study with highest values in July and October–December. This timing fits well with a previous study of French grunt larvae in St. Croix that showed peak settlement in May–June and October–November (McFarland et al. 1985). The 2–3 mo lag in their appearance in mangrove traps fits with the expected growth rate and ontogenetic shifts documented for this species (Shulman and Ogden 1987). Also of note, a September peak in catch of French grunts was observed in the 2018–2019 data. This would likely be the later stage juveniles from spring spawning events and indeed the modal size range of these fish was narrower than the fish from the 1991–1993 sampling period. Variations in mortality and recruitment as described above may have hampered detection of the expected early winter pulse of juveniles in traps in 2019.

Other species for which seasonal catch data are available from both periods include schoolmaster and yellowtail snapper. Yellowtail snapper >75 mm TL arrived in the mangrove catch in August through December in both sampling periods. This fits the expectations based on peak settlement seasons reported in the region and the delay in arrival at mangroves due to ontogenetic shifts (Rooker and Dennis 1991, Watson et al. 2002). Schoolmaster snapper also exhibited consistent seasonal peaks in catch in both sampling periods, from July through October. The seasonal timing and size class of schoolmaster snapper arrival in mangroves matches expectations from elsewhere in the region (Wormald et al. 2013).

Conclusions

There were several constraints imposed by the original study on the analysis and scope of these findings that warrant additional consideration. First, the original study occurred in two bays on one island, and therefore, inferences are limited geographically. However, the true value of these data is not in their spatial scope, it is in the rare temporal perspective enabled by a data set collected 25 YA. Second, sample size was dramatically different in the two periods. This was by design given the results of the initial study which yielded extremely small standard errors in their parameter estimates, no indication of differences within bay/side combinations (i.e., among traps along the same stretch of coast), and seasonal effects for dominant species that could have been detected with less frequent effort. Analyses accounted for the difference in effort by using measures such as CPUE, per-trap averages and standard error, and rarefaction, all of which inherently conduct comparisons at standardized units of effort. Third, due to the loss of the original trap-level data, only summary statistics from the publications are available to support comparative statistical analyses. This can be a common problem in studies relying on historical data from fiscally challenged agencies in developing regions (Smith et al. 2008). It may be desirable to explore techniques such as time-series analysis or multivariate techniques, but the required raw data are not available for both periods. Raw data from the present study are now electronically archived and publicly available to prevent this difficulty in the future (Kendall et al. 2019).

The stressors and threats to mangrove habitat in Salt River Bay were summarized in Tobias et al. (1996). Unfortunately, the same issues continue to be of concern 25 yrs later and require ongoing vigilance. These include: runoff of sediment and pollutants from the large watershed discharging into Sugar Bay, elevated fecal coliform bacteria in a couple of locations, potential enlargement of the marina, increases in vessel traffic, long-term tying/mooring to mangroves by boats (one was observed tied to the same trees for the entire duration of the 2018–2019 study), and extended camping and use of mangroves as shelter and campfire materials. It remains a challenge to quantify the relative extent to which each of these factors and others, such as changes in regional fish assemblages (Adams 2001, Pittman et al. 2014) and the 2011 emergence of nuisance sargassum blooms (Langin 2018), have contributed to the changes in the mangrove community documented here.

According to an FAO estimate, the US Virgin Islands lost 57% of their mangroves between 1980 and 2005 (FAO 2007), a figure that does not include the largest losses in St. Croix at Krause Lagoon in the 1960s. A more recent study suggested that mangrove coverage was more stable at least from 2000 to 2012 (Hamilton and Casey

2016), but this does not encompass the early or late years of our study and lacks the recent and near total demise of the Great Pond Bay mangroves in 2017 due to drought and channel blockage (Durdall 2018). On the entire island of St. Croix, the mangroves in Salt River Bay represent one of two remaining stands of healthy mangrove habitat with open access to ocean waters. The mangroves of Salt River Bay in particular are in close proximity to major reef features including a deep canyon with extensive coral habitat. This canyon, the surrounding reefs, walls, and drop offs encompass one of the most popular diving and fishing locations around St. Croix. The mangroves may be directly enhancing fish populations in the canyon for those species that undertake ontogenetic habitat shifts and even more broadly be an asset at the scale of the entire island (Nagelkerken et al. 2002, Mumby et al. 2004, Martin et al. 2015, Serafy et al. 2015, Shideler et al. 2017). Even if other habitat types are available for juvenile fishes, mangroves may support greater density and faster growth of fishes than other types of habitat (Adams et al. 2006, Dahlgren et al. 2006, Mateo et al. 2011), making protection of the remaining stands in St. Croix of special importance for maintaining productive and diverse fish populations.

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