Hurricane Maria in Puerto Rico: Effects on Reservoir Water Quality and Fish Community Structure and Resilience

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Abstract: Hurricane Maria, a Category 4 storm with sustained winds of 249 km h^{-1}, made landfall on Puerto Rico on 20 September 2017. The extreme precipitation resulting from this hurricane, combined with already saturated soil and the steep, mountainous terrain of the island, led to historic flooding across most of Puerto Rico. Reservoirs in many of the river systems on the island were preemptively drawn down in an attempt to absorb the volume of floodwaters but were quickly overwhelmed. Since many of these reservoirs had been the focus of previous studies, a rare opportunity arose to evaluate how extreme flooding affects lentic systems. We sampled seven of Puerto Rico's 13 large reservoirs in April and May 2018 using previously-used, published methodologies to compare pre- and post-hurricane characteristics of water quality and fish communities. Average discharge from reservoirs during the 24-h period of the day of the hurricane ranged 64–1807 m^3 sec^{-1} with a peak discharge of 5097 m^3 sec^{-1}, or 827 times annual mean flow. Ammonia and specific conductance increased post-hurricane, mean temperature and nitrate decreased, and other water quality parameters remained unchanged. Sport fish communities showed minimal differences between pre- and post-hurricane samples in all island reservoirs except for Loiza Reservoir, which largely collapsed post-hurricane with the primary sport fish species, butterfly peacock bass (*Cichla ocellaris*), disappearing from the reservoir. Other sport fish species decreased in abundance and maximum size, while invasive species were less affected. The hydraulic residence time of Loiza Reservoir during the hurricane averaged about 1 h, indicating the reservoir changed its entire volume of water nearly 24 times in a 24-h period. Our research concluded that extreme flood events resulting from hurricanes may influence reservoir fisheries and water quality under certain circumstances, although many systems may handle these perturbations with resilience.

Key words: discharge, disturbance, retention, community, flushing

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Extreme weather events such as hurricanes, flooding, drought, and forest fires are increasing in frequency and severity as global climate change progresses (Palmer and Räisänen 2002). These disturbance events have significant ecological consequences on the affected biotic communities (Pounds et al. 1999). Aquatic ecosystems are particularly susceptible to extreme weather events with flooding being a primary cause of natural disturbance. Although relatively well studied for lotic systems (e.g., Kozlowski 1984, Junk et al. 1989, Poff 1992), the influence of severe flooding on the biota of lentic waterbodies has received less attention.

Hurricane Maria made landfall on 20 September 2017 near Yabucao, Puerto Rico, as a strong Category 4 hurricane with wind speeds sustained at 249 km h^{-1} and up to 1 m of total rainfall over much of the island. Steep mountainous terrain, combined with rainfall rates in excess of 137 mm h^{-1} and soils saturated from Hurricane Irma that occurred two weeks earlier, led to extreme flooding across much of the island, exceeding historical flood records. For example, a USGS gage (500438800) on the Río La Plata at Comerio reported an official height of 10.6 m before the gage failed, exceeding the previous record of 8.9 m. It is unclear how high the river rose after the gage failed. This river was near its mean discharge about 4.4 m^3 sec^{-1} on 19 September when rains from Hurricane Maria began to fall, and discharge was rapidly approaching 2,700 m^3 sec^{-1} when the gage failed less than 24 h later. The previous highest recorded discharge at this gage was 762 m^3 sec^{-1}, during Hurricane Georges in 1998 (USGS 2018).

Many Puerto Rico river systems are impounded. Although most reservoirs were partially dewatered prior to hurricane landfall, flows resulting from the hurricane were sufficient to fill and flush the receiving reservoirs in a matter of hours for even the largest reservoirs on the island. For example, mean discharge of the La Plata River below the La Plata Reservoir Dam (gage 50045010) from the year prior to the hurricane was 1.08 m^3 sec^{-1}. During the hurricane, flow peaked at 5091 m^3 sec^{-1}, which was about double the mean discharge of the Missouri River at the Mississippi River confluence at St. Louis, Missouri (USGS 2009), and would have completely flushed La Plata Reservoir in less than two hours (Soler-López 2001b).

A few studies have addressed the influence of moderate flood events on reservoirs (e.g., Godlewsha et al. 2003) and the influence

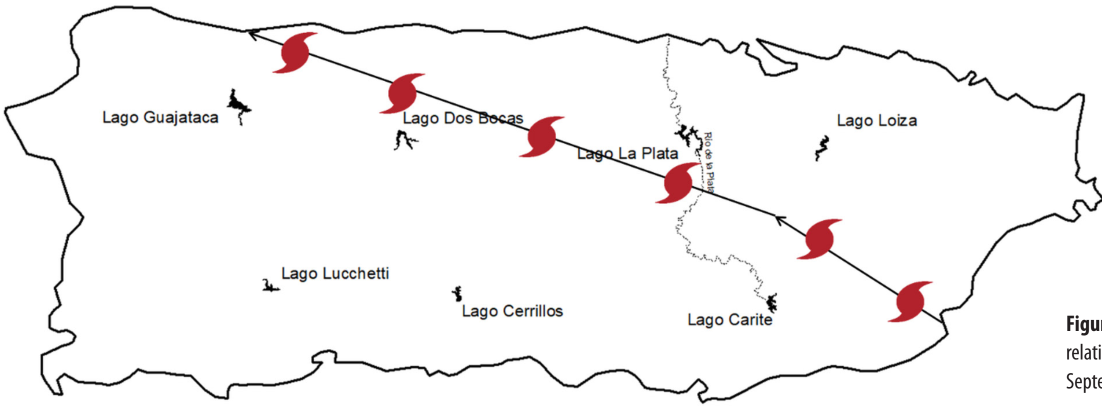

Figure 1. Location of study reservoirs in Puerto Rico relative to the center track of Hurricane Maria on 20 September 2017.

of high flow and elevated water level on invertebrates (Dirnberger and Thelkeld 1986) and fish (e.g., Sammons et al. 2002, Carlson et al. 2016). However, the effects of hydrological perturbations on lentic aquatic habitats and biotic communities of the magnitude experienced during Hurricane Maria have never been evaluated. Ecological disturbance plays a significant role in structuring biotic populations and ecosystem characteristics, and major disturbances can have profound impacts (e.g., Stanley et al. 2010). This hurricane may have flushed large numbers of organisms out of reservoir systems, transported large quantities of sediment and debris into these waterbodies, and potentially reshaped the reservoir basin itself. The flushing of reservoirs may reset the balance of desirable sport fish communities, or it may facilitate further establishment and dominance of invasive fish species (e.g., Sakai et al. 2001), which have been expanding at alarming rates in Puerto Rico (Neal et al. 2009).

Hurricane Maria presented an unprecedented opportunity to evaluate how extreme flooding affects lentic systems. Understanding resilience of native and introduced sport fish species to ecological disturbance, as well as assessing how recently established invasive species respond to these events has important implications for ecological stability and dynamics in aquatic systems. For Puerto Rico reservoirs in particular, management of recreational fisheries will depend on how important sport fish species and detrimental invasive species respond following the event. The goal of this research was to provide a rapid evaluation of the hurricane's effects on fish communities and water quality. Specifically, our objectives were to 1) estimate flood intensity that occurred during the hurricane and understand the hydrological dynamics within reservoirs, 2) assess changes to reservoir water quality following the disturbance event, and 3) compare fish population and community structure from pre- and post-catastrophic flood event.

Methods

Study Reservoirs

This research was conducted in seven of Puerto Rico's 13 major reservoirs. Fish community assessment was conducted in five reservoirs (Carite, Cerrillos, Dos Bocas, Guajataca, and Loiza) that provided representative geographic coverage of the island's lentic waterbodies (Figure 1). Pre-hurricane data on fish communities were available for each system. Long-term and hurricane-specific mean discharge data were available for all but Carite Reservoir, which lacked data during the majority of the hurricane. La Plata Reservoir is located on the same river system about 55 river km downstream of Carite Reservoir, and this reservoir was examined as a surrogate for calculation of hydraulic retention time effects. Pre-hurricane water quality data were available from Cerrillos, Dos Bocas, Lucchetti, and Guajataca reservoirs. These four systems were used for water quality comparisons pre- and post-hurricane.

Estimated Flooding Intensity

Public data from the USGS Caribbean-Florida Water Science Center's Puerto Rico website (USGS 2018) were used to calculate discharge rate (m^3 sec^{-1}) and hydraulic retention times (HRTs) for Puerto Rico reservoirs for the previous 10–16 years prior to hurricane, during the 24-h period of the hurricane, and during peak hurricane flow. The center of the hurricane made landfall at 0615 hours on 20 September 2017, and we used streamflow data from 0015 hours on 20 September to midnight of the same day to calculate hurricane-specific 24-h discharge. This period was identified as the period of greatest precipitation and associated discharge using visual inspection of the data. Reservoir details, including general statistics and water characteristics immediately prior to and during the hurricane are presented in Table 1.

Hydraulic retention times for each reservoir were calculated as

Table 1. Reservoir basin and discharge characteristics during Hurricane Maria. Discharge data were not available for Carite Reservoir during Hurricane Maria; La Plata Reservoir data were used as a surrogate. Stream gages at Guajataca and La Plata dams failed during the hurricane; time of final reading is presented. *DNF* indicates gages that did not fail, "Interm." indicates gages that operated intermittently during peak flow. Data on basin characteristics were obtained from Soler-López (2001b, 2011, 2012) and Soler-López and Gomez-Gomez (2005); data on discharge and water level obtained from USGS (2018).

Reservoir characteristics	Carite	Cerrillos[a]	Dos Bocas	Guajataca[b]	La Plata[c]	Loiza[d]	Lucchetti[b,d]
Year of construction	1913	1992	1942	1928	1974	1953	1952
Surface area (km^2)	1.20	2.49	1.78	3.42	3.09	2.67	1.11
Drainage area (km^2)	20.5	45.1	310.0	79.8	469.0	538.0	44.8
Original capacity (10^6 m^3)	13.95	38.03	37.50	48.46	40.21	26.81	20.35
Most recent capacity estimate (10^6 m^3)	10.74	37.26	16.74	42.28	35.46	17.53	10.21
Year of recent estimate	1999	2008	2010	1999	1998	2004	2014
Rate of storage loss (10^6 m^3 y^{-1})	0.037	0.046	0.341	0.087	0.198	0.308	0.12
Mean discharge (m^3 sec^{-1})	0.47	1.08	12.61	1.29	6.16	10.64	0.80
Full-pool spill water level (m MSL)	543.6	186.3[e]	89.9	196.9	52.0	41.1	53.00
Pre-hurricane level (m MSL, 1 day prior)	543.0	172.4	85.9	195.9	47.5	35.7	51.70
Peak-hurricane water level (m MSL)	544.6	178.9	96.3	199.5	51.8	38.3	53.90
Hurricane mean discharge (m^3 sec^{-1})	–	64.0	482.5	66.1	1240.1	1806.8	28.43
Hurricane peak discharge (m^3 sec^{-1})	–	81.8	1359.2	305.8	5097.0	3907.7	628.63
Time of observed discharge peak	–	2100 h	1245 h	1941 h	0900 h	1400 h	1845 h
Time at final reading before failure	–	DNF	DNF	1941 h	1100 h	DNF	Interm.

a. Cerrillos Reservoir stores floodwaters for slow release over time. Discharge averaged 89.2, 106.2, and 69.1 m^3•s^{-1} on September 21, 22, and 23, respectively.
b. Stream gage failed during Hurricane Maria and discharge rates are underestimated.
c. Loiza is the only reservoir with radial gates. All other reservoirs are equipped with simple spillways.
d. Gage located above reservoir.
e. Emergency spill level. This level has never been reached.

$HRT = V_t / T$, where *HRT* is the hydraulic retention time, V_t the volume of the reservoir at time *t*, and *T* is water loss in terms of discharge (Dodds and Whiles 2010). The V_t was calculated as the most recent published storage capacity at conservation pool adjusted by the product of the number of years since the last estimate and the published annual rate of capacity lost due to sedimentation (Table 1). We calculated average retention times using discharge data from the previous 10–16 years (through 2016) as available. To gain insight on how flows during the hurricane deviated from normal flows, we calculated hurricane-specific HRTs for the 24-h period defined previously.

Water Quality

Neal et al. (2014) evaluated Lucchetti, Cerrillos, Guajataca, and Dos Bocas reservoir water quality parameters in 2010. We repeated these procedures in May 2018 for comparison of pre- (May 2010) and post-Maria summer conditions. All reservoirs were sampled for *in situ* water quality parameters of temperature (C), dissolved oxygen (mg L^{-1}), turbidity (NTU), specific conductance (µS), and pH using a Hydrolab DS5 multiparameter data sonde (OTT HydroMet, Loveland, Colorado). Continuous surface sampling was used to provide high precision in parameter estimates for the entire reservoir (see Neal et al. 2014 for design).

Still following Neal et al. (2014), we collected 10 duplicate surface water samples for nutrient analysis: specifically, nitrate-N (NO_3), ammonia-N (NH_3), and soluble reactive phosphate (PO_4). Samples were collected in 250-ml polyethylene containers (Fisher Scientific International, Inc., Hampton, New Hampshire) and were immediately acid-preserved with 0.125 ml of 49% sulfuric acid (H_2SO_4) solution and refrigerated for a maximum of four days before processing (Baker et al. 2018). Samples were subsequently transported on ice to the Water Quality Analysis Laboratory at the University of Puerto Rico, Río Piedras, Puerto Rico (see Neal et al. 2014 for laboratory techniques).

Fish Communities

Pre-hurricane data were collected using standardized boat-mounted boom electrofishing (e.g., Neal et al. 1999, 2001, 2016; PRDNER 2007). The electrofishing vessel consisted of a 4.8-m boat equipped with a GPP 7.5 electrofishing box and 7500-W generator (Smith-Root, Inc., Vancouver, Washington). For consistency, we used only data that met the following sampling criteria. Target output power was 3500 to 5000 W and 3 to 5 A. All pre-hurricane samples were collected March to July using a minimum of 60 min and a maximum of 120 min of on-time electrofishing effort. Sampling design varied somewhat among reservoir samples, ranging from 6 to 12 stations and 10 to 15 min of on-time effort per station.

Post-hurricane data were collected at the end of April 2018, about 7 months after Hurricane Maria. We used equivalent electrical output for 10-min duration at 10 stations per reservoir to provide community data for comparison. All fish were collected, identified, and total length was measured to the nearest mm before returning to the reservoir unharmed. Threadfin shad (*Dorosoma petenense*) are a schooling species and electrofishing is not recommended for quantitative assessment (Boxrucker et al. 1995, Prchalová et al. 2012), therefore this species was collected to confirm presence/absence only. This research followed Mississippi State University IACUC Protocol 18-086.

Data Analysis

Analyses of overall changes in water quality and nutrient data consisted of a repeated measures ANOVA (F) with the water quality/nutrient parameters as the within groups factor and lake as between groups factor. Individual differences were detected using a Tukey's analysis (Z).

To visualize changes in species composition, we used Morisita's index of overlap (Morisita 1962), a similarity index calculated as:

$$CD = \frac{2\sum_{i=1}^{S} x_i y_i}{\left(\frac{\sum_{i=1}^{S} x_i^2}{x^2} + \frac{\sum_{i=1}^{S} y_i^2}{y^2}\right) XY},$$

where x_i is the number of times species i is represented in the total number X from sample x, y_i is the number of times species i is represented in the total number Y from sample y, D_x and D_y are the Simpson's index values for the samples x and y, respectively, and S is the number of species. The Simpson's index value is defined by:

$$D = \frac{\sum n(n-1)}{N(N-1)},$$

where n is the number of individuals of a particular species, and N is the total number of individuals of all species (Morisita 1962). Morisita's index of overlap generally provides values ranging from 0 (no overlap) to 1 (complete overlap). Thus, $1 - C_D$ is the proportion of the two samples that does not overlap, *ergo* dissimilarity.

Relative abundance (catch per effort) and size distributions of each fish species in each reservoir were compared from before and after the hurricane using Wilcoxon signed rank tests (W) and Kolmogorov-Smirnov tests (D), respectively. For each reservoir, all species except threadfin shad were pooled as 1) sport fish or 2) invasive species and we used Fisher's method (χ^2) to combine statistical results from species per reservoir to examine overall effects within reservoir (Rosenthal 1978, Kost and Dermott 2002). All tests were two-tailed using alpha = 0.05, with alpha = 0.10 indicating marginal significance.

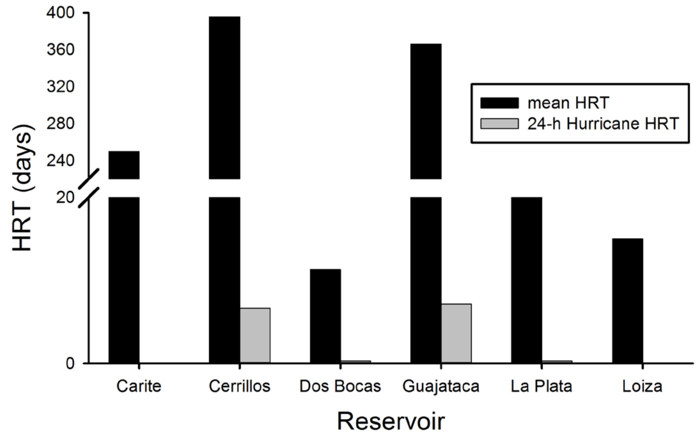

Figure 2. Reservoir hydraulic retention times (HRTs) averaged across previous 10–16 years and during a 24-h period during Hurricane Maria. HRTs for hurricane were based on discharge during the period beginning 6 h before landfall and ending 18 h after landfall. Values based on storage capacities were adjusted for sedimentation and assume reservoirs were at full pool. Stream gages failed in Guajataca and La Plata reservoirs during the hurricane, and thus incomplete discharge estimates may have resulted in overestimation of the 24-h HRT calculations.

Results

Estimated Flooding Intensity

Mean discharge rate from Puerto Rico reservoirs ranged 0.8 to 12.6 $m^3 sec^{-1}$ over previous 10–16 years. During the 24-h period encompassing Hurricane Maria landfall, mean discharge ranged 28.4 to 1806.8 $m^3 sec^{-1}$, although lower values represented gages that malfunctioned during the storm or were affected by storage of floodwaters for slow release (Table 1). Peak discharge was as high as 5097 $m^3 sec^{-1}$. Average HRTs ranged from more than 1 year (395 d) in Cerrillos Reservoir to 15 d in Dos Bocas Reservoir. During the hurricane, 24-h HRTs ranged from about 7 d in Guajataca Reservoir to just over 2 h in Loiza (Figure 2).

Water Quality

Pre- and post-hurricane water quality differed overall ($F = 5843$, df = 1, 4, $P < 0.01$) and for several parameters following Hurricane Maria in the four reservoirs (Table 2). Temperatures post-hurricane were cooler ($Z = 156.3$, $P < 0.01$), likely due to natural variability. Specific conductance was higher post-hurricane in all reservoirs, suggesting that sediment inputs during flooding increased dissolved solid concentrations ($Z = -5.40$, $P < 0.01$). Dissolved oxygen ($Z = -2.41$, $P = 0.25$) and mean pH ($Z = 2.47$, $P = 0.22$) were similar between pre- and post-hurricane periods and showed no clear trends. The concentration of ammonia increased across all reservoirs compared to pre-hurricane; this increase was marginally significant ($Z = 2.78$, $P = 0.06$) and likely due to increased organic matter

Table 2. Summary data (SE) for pre- and post-hurricane water quality in four Puerto Rico reservoirs. All parameters measured at 0.3 m of reservoir surface.

Parameter	Cerrillos		Dos Bocas		Guajataca		Lucchetti	
	Pre	Post	Pre	Post	Pre	Post	Pre	Post
Temperature (C)	29.4	27.2	30.3	28.8	29.7	28.4	29.5	28.1
	(0.01)	(0.00)	(0.02)	(0.01)	(0.01)	(0.00)	(0.01)	(0.00)
DO (mg L^{-1})	10.1	8.8	13.1	13.4	10.0	11.0	13.7	8.2
	(0.07)	(0.01)	(0.06)	(0.02)	(0.03)	(0.00)	(0.03)	(0.00)
Turbidity (NTU)	26.6	n/a	60.5	n/a	26.8	n/a	139.4	n/a
	(0.5)	n/a	(2.1)	n/a	(1.1)	n/a	(15.9)	n/a
Spec. Cond. (µS)	197.5	246.3	156.9	200.2	221.0	240.1	210.1	262.8
	(0.09)	(0.03)	(0.15)	(0.15)	(0.10)	(0.04)	(0.05)	(0.03)
pH	8.70	8.45	9.06	9.16	8.51	8.23	9.04	8.42
	(0.01)	(0.00)	(0.01)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)
NH_3 (mg L^{-1})	0.008	0.103	0.023	0.079	0.046	0.103	0.039	0.089
	(0.002)	(0.010)	(0.003)	(0.007)	(0.007)	(0.009)	(0.005)	(0.015)
NO_3 (mg L^{-1})	0.050	0.012	0.378	0.018	0.050	0.019	0.080	0.013
	(0.002)	(0.004)	(0.106)	(0.001)	(0.003)	(0.000)	(0.004)	(0.000)
PO_4 (mg L^{-1})	0.015	0.007	0.057	0.010	0.014	0.013	0.017	0.011
	(0.004)	(0.001)	(0.012)	(0.001)	(0.002)	(0.004)	(0.001)	(0.000)

decomposition with debris deposited by both floodwaters and the wind event. Concentrations of nitrate ($Z = -6.22$, $P < 0.01$) increased, but phosphate ($Z = -0.67$, $P = 0.98$) did not change appreciably.

Fish Communities

Changes in fish communities from before and after Hurricane Maria were evident in varying degrees. Dos Bocas Reservoir displayed a community that was 43% dissimilar, followed by Loiza Reservoir that was 29% dissimilar (Figure 3), while Carite, Cerrillos, and Guajataca reservoirs demonstrated sport fish communities more consistent with pre-hurricane data. Comparisons of relative abundance and size distributions from before and after the hurricane are presented below. Results are separated into sport fish, threadfin shad (prey), and invasive species, and comparisons for each reservoir are described. Scientific names of these species are presented in Table 3, which also presents a visual representation of these data, with mean TL as an indicator of size distributions.

Sport Fish.—Relative abundance of principle sport fish, measured as CPUE, remained unchanged in Carite Reservoir following the hurricane ($\chi^2 = 15.04$, $P = 0.77$). A native species, bigmouth sleeper, dominated the catch both before and after the hurricane, with no difference in catch rate ($W = 4.5$, $P = 0.50$). Other species targeted by anglers also exhibited no statistical differences in relative abundance from before or after the hurricane. Size distribu-

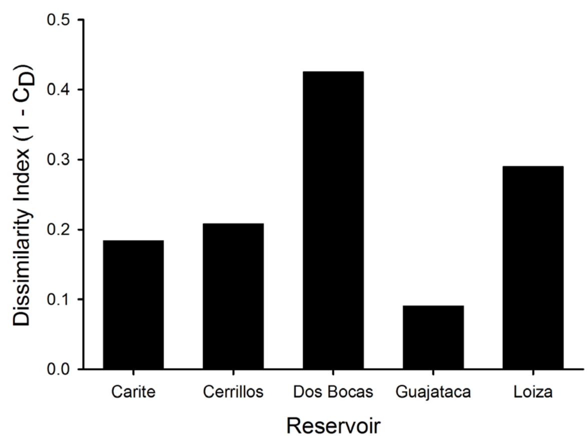

Figure 3. Dissimilarity (1 – C_D) between pre- and post-hurricane fish communities in Puerto Rico reservoirs. C_D is Morisita's index of similarity.

Table 3. Catch-per-effort (CPUE), mean TL (mm), and standard deviation (SD) of mean TL for pre- and post-hurricane (pre → post) fish communities in five Puerto Rico reservoirs. Threadfin shad relative abundance is not sampled effectively with electrofishing; this species is listed only as present (P) or not collected (NC); n/a indicates 'not applicable.'

	Carite	Cerrillos	Dos Bocas	Guajataca	Loiza
Species	[CPUE] Mean TL (SD)	[CPUE] Mean TL (SD)	[CPUE] Mean TL (SD)	[CPUE] Mean TL (SD)	[CPUE] Mean TL (SD)
Bluegill (*Lepomis macrochirus*)	[6.0 → 3.0]	–	–	–	–
	123.4 → 117	–	–	–	–
	(18.6 → 19.8)	–	–	–	–
Blue tilapia (*Oreochromis aureus*)	–	–	[38.0 → 1.7]	[10.7 → 12.5]	–
	–	–	227.8 → 253.3	191.8 → 171.4	–
	–	–	(23.3 → 57.1)	(34.9 → 72.1)	–
Bigmouth sleeper (*Gobiomorus dormitor*)	[32.0 → 20.9]	–	–	–	–
	204.8 → 243.3	–	–	–	–
	(78.2 → 47.2)	–	–	–	–
Butterfly peacock bass (*Cichla ocellaris*)	[2.7 → 0.6]	–	[4.0 → 9.3]	[3.6 → 6.6]	[13.8 → 0.0]
	1.38 → 247	–	300.5 → 259.6	224.5 → 258.4	369.5 → n/a
	(28.8 → n/a)	–	(88.9 → 107.6)	(80.0 → 72.2)	(90.4 → n/a)
Channel catfish (*Ictalurus punctatus*)	[1.3 → 0.0]	–	[7.0 → 0.0]	–	[3.0 → 0.6]
	269.0 → 0	–	311.9 → n/a	–	332.0 → 334
	(118.8 → n/a)	–	(89.1 → n/a)	–	(37.9 → n/a)
Redhead cichlid (*Viejas melanura*)	–	–	–	[25.7 → 33.0]	–
	–	–	–	189.5 → 200.3	–
	–	–	–	(29.4 → 55.8)	–
Jaguar guapote (*Parachromis managuensis*)	–	–	[10.0 → 4.6]	–	[24.1 → 13.6]
	–	–	250.3 → 313.5	–	249.4 → 113.8
	–	–	57.6 → 29.6)	–	(82.6 → 84.2)
Largemouth bass (*Micropterus salmoides*)	[3.3 → 7.8]	[73.4 → 124.0]	[9.0 → 0.0]	[0.0 → 13.2]	[0.0 → 1.8]
	385.8 → 301.8	247.7 → 284.8	430.6 → n/a	n/a → 423.8	n/a → 130.3
	(122.3 → 106.2)	(116.9 → 77.7)	(41.4 → n/a)	(n/a → 73.6)	(n/a → 104.5)
Mozambique tilapia (*Oreochromis mossambicus*)	[0.7 → 0.0]	–	[13.0 → 0.6]	–	[98.5 → 2.4]
	92.0 → n/a	–	265.3→ 257	–	249.7 → 114.3
	(n/a → n/a)	–	(27.7 → n/a)	–	(58.8 → 22.8)
Red devil cichlid (*Amphilophus labiatus*)	–	–	[62.0 → 13.3]	[20.3 → 18.3]	[33.5 → 23.0]
	–	–	162.7 → 137.0	211.8 → 183.2	175.3 → 115.5
	–	–	(44.6 → 16.6)	(30.6 → 67.9)	(21.6 → 50.7)
Redbreast sunfish (*Lepomis auritus*)	[26.0 → 1.2]	[1.3 → 6.6]	–	–	–
	163.2 → 177.3	57.8 → 144.9	–	–	–
	(38.0 → 67.3)	(11.0 → 38.2)	–	–	–
Redbreast tilapia (*Coptodon rendalli*)	[2.7 → 1.2]	[58.2 →15.0]	[1.0 → 1.2]	[8.9 → 4.4]	[4.9 → 11.2]
	253.3 → 132.5	263.7 → 72.1	216 → 85.0	169.3 → 107.7	193.8 → 115.3
	(16.0 → 128.0)	(15.4 → 44.9)	(n/a → 8.5)	(17.5 → 58.1)	(53.5 → 23.6)
Redear sunfish (*Lepomis microlophus*)	[3.3 → 6.0]	[29.7 → 8.4]	–	–	–
	250.6 → 212.5	144.8 → 165.7	–	–	–
	(36.9 → 42.1)	78.8 → 41.6)	–	–	–
Amazon sailfin catfish (*Pterygoplichthys pardalis*)	[0.0 → 1.8]	[n/a → 0.6]	[46.0 → 87.0]	[1.8 → 16.8]	[88.6 → 76.6]
	n/a → 432.0	n/a → 397	370.8 → 355.7	265.7 → 362.2	371.1 → 389.5
	(n/a → 95.5)	(n/a → n/a)	(57.1 → 48.0)	(74.1→ 89.5)	(57.1 → 52.1)
Threadfin shad (*Dorosoma petenense*)	[P → NC]	[P → P]	[P → P]	[P → NC]	[P → NC]
White catfish (*Ameiurus catus*)	[3.3 → 1.2]	[5.6 → n/a]	–	[0.0 → 0.7]	–
	192.8 → 130	147.5 → n/a	–	n/a → 408	–
	(54.6 → 107.5)	(86.2 → n/a)	–	(n/a → n/a)	–
Total catch (*n*)	121 → 76	508 → 258	152 → 203	119 → 156	541 → 223

tions increased overall in Carite Reservoir ($\chi^2 = 15.04$, $P = 0.77$), with three species displaying increases in size distribution post-hurricane that were significant or marginally significant (redear sunfish: $D = 0.8$, P < 0.01; bigmouth sleeper: $D = 0.38$, $P = 0.06$; largemouth bass: $D = 0.64$, $P = 0.09$).

Cerrillos Reservoir also avoided major effects from the hurricane in terms of relative abundance ($\chi^2 = 17.00$, $P = 0.15$). The only species displaying a significant change in catch rate was redbreast tilapia (catch rate declined, $W = 15$, $P = 0.05$). Overall, distributions of sport fish species shifted to larger sizes ($\chi^2 = 19.2$, $P < 0.01$), and this shift was driven by largemouth bass ($D = 0.18$, $P < 0.01$) and redbreast sunfish ($D = 0.92$, $P = 0.01$).

Catch rates in Guajataca Reservoir also were consistent with pre-hurricane samples ($\chi^2 = 15.51$, $P = 0.63$). No differences were detected in length distributions of sport fish ($\chi^2 = 12.32$, $P = 0.38$), with the exception of redbreast tilapia, which declined in size ($D = 0.83$, $P < 0.01$).

Despite displaying the highest level of fish community dissimilarity between pre- and post-hurricane conditions, Dos Bocas Reservoir was largely unaffected in terms of catch rates or size distributions of sport fish species. Pooled relative abundances in Dos Bocas Reservoir were similar between before and after Hurricane Maria ($\chi^2 = 6.15$, P = 0.36), with no differences in relative abundance observed for individual sport fish species. Further, no differences were detected in length distributions of sport fish ($\chi^2 = 14.32$, $P = 0.25$).

Loiza Reservoir, on the other hand, displayed substantial changes in sport fish after the hurricane. Relative abundance declined for pooled species ($\chi^2 = 32.44$, $P = 0.02$), driven primarily by butterfly peacock bass ($W = 36.0$, $P = 0.01$) and Mozambique tilapia ($W = 14.0$, $P = 0.10$). Butterfly peacock bass were abundant in Loiza reservoir prior to Hurricane Maria, yet not a single individual was collected or observed seven months post-hurricane. Size distributions of the fish community shifted to smaller individuals ($\chi^2 = 27.62$, $P < 0.01$), driven by redbreast tilapia ($D = 0.80$; $P < 0.01$).

Threadfin Shad.—Threadfin shad were abundant in all reservoirs prior to Hurricane Maria, but were not collected during post-hurricane sampling in Carite Reservoir, Guajataca Reservoir, or Loiza Reservoir. Threadfin shad were collected in Cerrillos Reservoir and Dos Bocas Reservoir during both pre- and post-hurricane samples.

Invasive Species.—The only invasive species collected in Carite Reservoir was Amazon sailfin catfish. This species was not collected during pre-hurricane sampling, and only three adult individuals were collected post-hurricane ($W = 3.00$, $P = 1.00$). Similarly, this is the only invasive occurring in Cerrillos Reservoir, and no fish were collected during pre-hurricane sampling, and only one individual was collected post-hurricane ($W = 0.00$, $P = 1.00$).

In Dos Bocas Reservoir, there was a marginally significant increase in pooled catch rate of all invasive species ($\chi^2 = 22.70$, $P = 0.09$), with Amazon sailfin catfish ($W = 1.5$, P = 0.07) and red devil cichlids ($W = 19.5$, $P = 0.07$) found in greater relative abundance post-hurricane. Jaguar guapote catch rate did not change ($W = 21.5$, $P = 0.62$). We observed a shift in Amazon sailfin catfish ($D = 0.24$, $P = 0.03$) and red devil cichlid ($D = 0.35$, $P = 0.04$) length distributions towards smaller sizes, while jaguar guapote were larger overall ($D = 0.80$, $P = 0.03$).

Guajataca Reservoir contained at least three invasive species, with no overall change in pooled relative abundance ($\chi^2 = 13.25$, $P = 0.37$). Amazon sailfin catfish displayed a marginally significant increase in relative abundance post-hurricane ($W = 2.0$, $P = 0.09$), while redhead cichlid ($W = 37.5$, $P = 0.60$) and red devil cichlid ($W = 16$, P = 0.83) did not change. Both Amazon sailfin catfish ($D = 0.86$, $P = 0.04$) and redhead cichlid ($D = 0.52$, $P < 0.01$) shifted toward larger sizes following the hurricane, while red devil cichlid ($D = 0.28$, $P = 0.18$) did not change.

Loiza Reservoir is home to at least three invasive species. Pooled catch rates of all three species were lower after the hurricane ($\chi^2 = 32.44$, $P = 0.02$), although these declines were not statistically significant at the species level (Amazon sailfin catfish: $W = 37.0$, $P = 0.36$; jaguar guapote: $W = 63.0$, $P = 0.34$; red devil cichlid: $W = 21.0$; $P = 0.27$). However, size distributions of all three species changed following the hurricane, with Amazon sailfin catfish size distribution shifting toward larger fish ($D = 0.21$, P = 0.003), while both jaguar guapote ($D = 0.69$, $P < 0.01$) and red devil cichlids ($D = 0.72$, $P < 0.01$) consisted of primarily juveniles post-hurricane.

Discussion

Climate change models consistently predict increases in climactic stochasticity (e.g., Sophocleous 2004, Hirabayashi et al. 2008, IPCC 2013), and there is an urgent need for research to develop comprehensive scientific approaches that address the impacts of episodic extreme weather events, including extreme flooding (Wantzen et al. 2008). The effects of drought and flooding have been frequently addressed for riverine systems (e.g., Junk et al. 1989; Lake 2000, 2003; Naiman et al. 2008; Power et al. 2008), but similar treatment for extreme events has not been given to lentic waterbodies. Many studies have demonstrated the importance of water level in determining size structure, reproduction, and community dynamics of species in lakes and reservoirs (e.g., Sammons et al. 2002, Neal et al. 2006, Gaboury and Patalas 2011, Tonkin et al. 2014, Chizinski et al 2015). Water level also has been shown to affect a number of biological, physical, and biogeochemical properties of reservoirs (e.g., Quennerstedt 1958, Fabre and Patau-Albertini 1986, Wagner and Falter 2002, Nowlin et al. 2004, Furey et al. 2009), with direct and indirect impacts on fish and fisheries. However, we found no literature to indicate that the effects of flow and water replacement of this magnitude on reservoir physicochemical environment and fish communities has been studied prior to Hurricane Maria.

Although the HRTs calculated for Puerto Rico reservoirs during Hurricane Maria are exceptionally short compared to long-term averages, they are in fact overestimates of what actually occurred. Cerrillos Reservoir stored floodwaters and then released them more slowly over several days following the hurricane. This resulted in lower discharge measurements and higher HRT calculations that do not accurately reflect the volume of floodwaters that this reservoir processed. Daily mean discharge rate in Cerrillos Reservoir continued to increase for several days after the hurricane as stored floodwaters were slowly released, averaging 89.2, 106.2, and 69.1 m^3 sec^{-1} on 21, 22, and 23 September respectively. Likewise, discharge data from Guajataca and La Plata reservoirs were interrupted during the storm by failure of the stream gages. Thus, it is likely that discharge was significantly greater than reported, leading to overestimation of HRT.

The estimate of HRT in Loiza Reservoir was an overestimate as well, as the calculation was based on the reservoir being at full pool during the hurricane, but this was not the case. To prepare for the hurricane, water was released from the radial gates beginning on 17 September, and reservoir water level dropped to more than 5 m below full pool as the storm intensified over the island (Figure 4). All gates were opened during the peak of the hurricane. During the 24-h period used in calculation of HRT, the reservoir water level averaged 37.95 m MSL. At this water level, the reservoir volume is about half of what it is at full pool (Figure 4). Thus, actual HRT during the hurricane was about 1 h, suggesting that this system exchanged its entire water volume 24 times during the 24-h period. Only the Loiza Reservoir dam had this design allowing water level to remain low during high flows.

Although some of the pre-hurricane data used for comparison in this study were collected many years before the hurricane, this was due to the stringent conditions placed on pre-data used for comparison. Fish population sampling in these reservoirs occurs frequently; however, collections often occurred outside of our sampling window or used gear settings that did not match our design. As such, the authors decided to use the most recent data that were comparable to our 2018 data. In cases where pre-data were older, we examined newer data that did not meet our inclusion standards to confirm that major community changes were not underway prior to the hurricane. With the exception of Dos Bocas Reservoir, where largemouth bass were gradually declining in abundance, fish communities were relatively stable in most reservoirs prior to 20 September 2017. Thus, we are comfortable that the pre-data provided the best available snapshot of each reservoir's fish community prior to the disturbance.

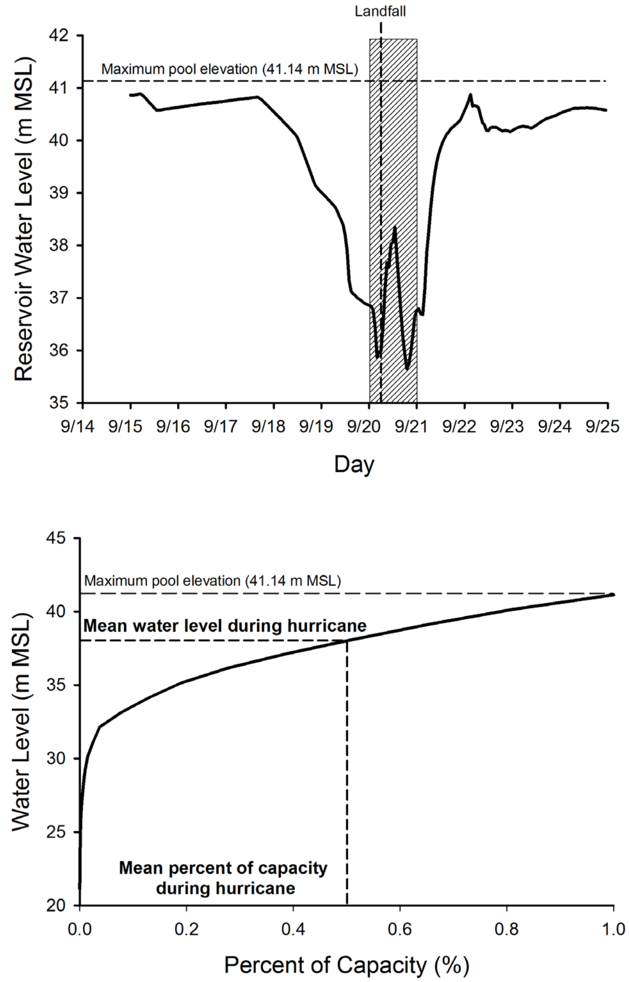

Figure 4. (Top:) Loiza Reservoir water level reduction prior to and during Hurricane Maria. Shaded area represents 24-h period used to estimate HRT during flood event. (Bottom:) Relationship between percent of total reservoir storage capacity and water level, with mean water level maintained during the 24-h HRT period (Data obtained from USGS 2018).

This study suggests that reservoir fish communities are typically resilient to extreme flushing events; however, under some circumstances they can be vulnerable to perturbation. Variability in catch rates is not uncommon for electrofishing, especially for cichlids, as they are less susceptible to the electric field (Holliman 1998, Bies et al. 2016). However, research has consistently demonstrated that variation in electrofishing catch rates is related to abundance for many fish species (e.g., Coble 1992, McInerny and Degan 1993, Rogers et al. 2003), thus the severe declines in catch rates of multiple species in Loiza Reservoir can be interpreted as a response of fish abundance to perturbation. This reservoir is unique among

Puerto Rico reservoirs in that it uses gated spillways with eight radial gate structures (Soler-López and Gómez-Gómez 2005), as opposed to the overflow spillway structures in other reservoirs. In those systems, flow occurs over rather than through the dam, and fish likely find refuge in the relatively static conditions provided by deeper waters and coves. Opening gates on Loiza Reservoir lowered the water level and dewatered more protected coves, and the extreme magnitude of the flow resulted in an extremely short HRT. This effectively converted the reservoir into a fast-flowing river. During the 24-h period encompassing landfall, the Loiza River that supplies the reservoir had an average and peak discharge of 1787 and 3908 $m^3 sec^{-1}$, respectively. To put this in perspective, this peak discharge was more than three times greater than the annual mean discharge of the Arkansas River, nearly half the annual mean discharge of the Ohio River, and 23% of the annual mean discharge of the Mississippi River (Kammerer 1990). The mean discharge rate of the Loiza River over previous decades was 10.6 $m^3 sec^{-1}$, thus peak flow during the hurricane was 367 times greater than average.

We do not believe the loss of fish was due to in-reservoir fish kills. Although hurricanes can significantly impair water quality and result in fish kills (Mallin et al. 1999), those kills co-occurred with severe water quality problems caused primarily by a combination of inputs of riparian swamp water, release of raw and partially treated sewage, and breaching of several swine waste lagoons. No fish kills were reported on Loiza Reservoir, and the likelihood that a water-quality related fish kill was responsible for the disappearance of fish is low considering that the other reservoirs received similar inputs of flow, sediment, and organic matter and were not affected.

The most likely scenario is that fish were involuntarily flushed or voluntarily migrated from the system. Peacock bass (*Cichla* spp.) prefer backwater habitat with relatively clear water, although they may traverse more lotic conditions to disperse (Winemiller 1997). The importance of flow in the migration and dispersion of fishes in rivers is well studied (e.g., Welcomme 1979, Reynolds 1983, Agostinho et al. 2004). Further, flows associated with major floods can entrain fish and move them downstream, particularly for very small- (Harvey 2011) and large-bodied fish (Smith and Kwak 2015). It is unknown if butterfly peacock bass and other species migrated via the flow or were simply swept from the reservoir.

Further, a number of studies have shown that disturbance, including extreme flood events (Havel et al. 2005), can increase the success of biological invaders (e.g., Dukes and Mooney 1999, Sakai et al. 2001). While sport fish species were lost from Loiza Reservoir, invasive species appeared to be more resilient. Amazon sailfin catfish were unaffected by the event, maintaining high abundance and even large body size. This species can utilize the lower velocities in the bottom boundary layer as well as hydrodynamic characteristics of their body form to stay in place during high flow events. Amazon sailfin catfish can also escape harsh weather events on land or in burrows, as they are capable of breathing air for up to 30 h (Hossain et al. 2018). Abundance and size structure of red devil cichlids and jaguar guapote declined post-hurricane, but this decline was not nearly as extreme as declines observed for the sportfish, especially butterfly peacock bass and Mozambique tilapia.

Conversely, research has demonstrated recovery of important sport fish species following disturbance (Yount and Niemi 1990). Sampling efforts by the Puerto Rico Department of Natural and Environmental Resources in August 2018 collected nine butterfly peacock bass in Loiza Reservoir that ranged from 250 mm to 362 mm TL (L. Olmeda, Puerto Rico Department of Natural and Environmental Resources, personal communication). The collection of these fish suggest that some juveniles were able to survive in the reservoir or were able to recolonize from tributaries or other adjacent water bodies. It appears that this species could recover, although it is unclear how overall community dynamics will change within the system. No threadfin shad have been collected in recent sampling, however, suggesting that a primary prey species may not be as resilient.

Water quality and habitat in the reservoirs were also impacted by Hurricane Maria. Specific conductance increased in all four reservoirs analyzed, likely due to substantial input of sediment and dissolved solutes associated with hurricanes (Gellis 1993). All reservoirs experienced extensive sedimentation of upper reaches and loss of reservoir surface area, although the magnitude of sedimentation was not assessed. Soler-López (2001a, 2001b) reported that sedimentation associated with Hurricane Hortense (1996) and Hurricane Georges (1998) filled 10% of Puerto Rico's reservoir original volumes. It is reasonable to assume similar or higher rates of sedimentation during Hurricane Maria. Sedimentation can change a reservoir's ecology, including phytoplankton (Holz et al. 1997), zooplankton (Popp et al. 1996), benthic communities (Popp and Hoagland 1995), and fishes (e.g., Gido et al. 2000). Along with high sediment loads, large quantities of terrestrial organic matter also entered reservoirs. During our surveys, whole stands of bamboo (*Bambusa* spp.) could be seen standing upright in offshore reservoir areas where they were deposited by incoming floodwaters, and trees and other structures had been blown into the littoral zone or each reservoir. Large influxes of organic matter can create high biological oxygen demand, reduce oxygen levels, and increase ammonia (e.g., Mallin et al. 1999) within a few weeks of deposition. Ammonia was significantly higher in our post-hurricane samples, but was well within safe limits.

This research examined how the extreme wind and flood events of Hurricane Maria influenced reservoir water quality and fish communities in Puerto Rico. While most reservoirs experienced limited effects, extreme flushing in one system clearly reduced abundance of larger fish and nearly eliminated important sport fish species. Invasive fish species displayed potentially greater resilience to perturbation, which could result in degradation of sport fisheries in the reservoirs. It is unclear whether sport fish populations will recover over a greater time period, although more recent samples suggest possible recovery of species nearly extirpated during the event. Negative water-quality effects were measurable but likely transitory; however, sedimentation appeared substantial and requires additional study to understand its influence on reservoir lifespan and overall habitat quality. Because events like Hurricane Maria are expected to increase in frequency and severity, managers should examine the vulnerability of their fisheries to extreme storm events in terms of reservoir operation and basin morphometry, design operational strategies to minimize impacts, and develop post-event recovery plans.

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