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Article

Limnological Response of Las Curias Reservoir, San Juan, Puerto Rico: Successful Management of the Invasive Aquatic Fern, *Salvinia molesta*

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Abstract: The anthropogenic deterioration of aquatic ecosystems affects water resources due to agricultural malpractices, pollution from domestic septic tanks, recreational activities, and poor watershed management, among other factors. This study examines the management of Las Curias Reservoir, San Juan, Puerto Rico, after the 2016 arrival of the invasive aquatic fern *Salvinia molesta*. In September 2019, a community-led initiative introduced the *Cyrtobagous salviniae* weevil, an effective biological control agent for *S. molesta*, and commenced a mechanical removal campaign using an aquatic harvester. Limnological sampling (September 2019 to September 2022) and drone flights were employed to measure physicochemical and floating plant cover changes, respectively, in the reservoir. Monitoring of weevils in the reservoir demonstrated rapid establishment and dispersal, which resulted in visible damage including browning of plants and eventually sinking of entire mats. From 23 July 2019, the reservoir surface was predominantly covered by salvinia, occupying an area of 17.7 ha (100% coverage). This coverage decreased to 12.6 ha (71%) by 29 January 2021. By 12 August 2022, the coverage had been substantially reduced to just 1.1 ha, representing only 6% of the reservoir surface. In 2022, the reservoir recorded an average dissolved oxygen concentration of 2.4 mg L^{-1} ($\pm$0.0, n = 144), the highest in the study period and indicative of ecosystem recovery. After three years of control efforts, dissolved oxygen, pH, and specific conductance returned to levels recorded prior to *Salvinia molesta* introduction. This ecosystem recovery, a first in Puerto Rico, could be attributed to early use of mechanical control and the long-term impact of biological control.

Keywords: biological control; *Cyrtobagous salviniae*; giant salvinia; gis; limnology; water quality

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1. Introduction

Altered aquatic ecosystems are prone to invasions of invasive species [1]. For example, the construction of dams and the subsequent urban developments increase loads of wastewaters to both lentic and lotic ecosystems, causing drastic shifts in trophic structure, food web complexity, and the displacement of natives by invasive species [2–4]. Once non-native species become established, important ecosystems services—including clean and abundant water, recreation, flood mitigation—are soon compromised, and management initiatives are required to recover ecosystem services. Management of non-native species in aquatic ecosystems involves the use mechanical, chemical, or biological controls [5,6]. Of these options, chemical controls are more restricted, particularly in water bodies used for water supply; therefore, mechanical and biological controls are normally preferred.

The exotic aquatic fern, *Salvinia molesta* (Salviniaceae) [7], also known as giant salvinia (hereby after referred to as salvinia), is one of the most invasive aquatic weeds in the United States and globally [8,9]. It is native to southern Brazil, Argentina, and Uruguay but has been introduced in tropical and subtropical areas around the world [10,11]. In 2013, salvinia was listed among the 100 most harmful invasive alien species in the world by the Species Survival Commission (SSC) of the International Union for Conservation of Nature (IUCN) [8]. Salvinia has a rapid growth rate and propagates through fragmentation, allowing it to easily disperse and colonize new habitats [12]. Under ideal conditions, the plant has the ability to form extensive layers of vegetation across the surface of lakes, ponds, reservoirs, and swamps [13,14]. The expansion of salvinia in water bodies can limit the growth of native species and reduce light penetration and dissolved oxygen below the mats, affecting water quality and ecosystem structure and service [15–17]. Rapid rates of nutrient uptake combined with relatively slow rates of decomposition enable salvinia to tie up nutrients that could be used by other primary producers that contribute to complex food chains [11]. Salvinia dominance in an lentic ecosystem can influence the overall structure of the aquatic environment [15]. It directly competes with submerged macrophytes and phytoplankton for nutrients and light. This can suppress their growth and alter the structure of those communities, and can potentially affect ecosystem services [18,19]. Submerged macrophytes can also create conditions unfavorable for phytoplankton, and potentially release allelopathic substances that inhibit their growth [20].

In 2016, salvinia, initially introduced to Puerto Rico through commercial trade, was detected in the Las Curias reservoir in suburban San Juan, Puerto Rico, and is now spreading to other water bodies [21]. Hurricane Maria in 2017 [22] accelerated its spread in Las Curias, probably due to eutrophication after an increase in nutrient-rich sewage discharges associated with septic tanks [23]. By July 2019, salvinia mats completely covered the reservoir, limiting all economic and ecological services [23]. Since September 2019, a community-driven strategy, in collaboration with the University of Puerto Rico at Rio Piedras (UPR-RP), Louisiana State University (LSU), and local and federal agencies, was initiated at Las Curias reservoir to develop a management strategy for salvinia. The strategy involved the use of biological and mechanical control methods. The biological control component involved the introduction of the salvinia weevil, *Cyrtobagous salviniae* [24], a host-specific herbivore that has been released in the United States, South Africa, Australia, and Asia [10]. Management of salvinia using the weevil has resulted in successful control of the plant in tropical and subtropical regions globally [12,25]. Due to the massive public outcry in San Juan, managers used mechanical removal with volunteers and eventually acquired an aquatic weed harvester. The use of harvesters is considered a short-term strategy and of limited use due to the ability of salvinia to double its mass in matter of days [25].

The overarching goal of this study was to document the changes in salvinia coverage and physicochemical responses of Las Curias reservoir during the salvinia control project. The specific objectives were to measure the temporal changes in surface coverage caused by salvinia, quantify the ecological quality of the reservoir, and establish a relationship among water quality and salvinia coverage. Reservoir baseline conditions before the control project showed that complete coverage of salvinia resulted in poor water quality, including reduced oxygen levels, lower light penetration, and reduced pH [23]. We predicted that a reduction in salvinia coverage would accelerate the increment of epilimnetic water temperature, dissolved oxygen, pH, and specific conductance, while also enhancing water transparency. Similarly, in regions below the epilimnion, we anticipated a gradual increase in specific conductance, temperature, and pH over time, aligning with the reduction in plant coverage. Regarding the biological control agent introduced, we predicted that the tropical climate of this region would allow a rapid population growth of the weevil and subsequent salvinia control. We also predicted that the combined effects of the biological and mechanical controls would speed up the reduction in salvinia coverage in the reservoir.

2. Materials and Methods

2.1. Site Description

The construction of the Las Curias reservoir was completed in 1946 and was operated by the Puerto Rico Aqueduct and Sewer Authority (PRASA) until the early 1980s. Located in the Cupey ward of San Juan, Puerto Rico, USA (N18.34169; W66.04828), the reservoir primarily served as a municipal water source [26,27]. Hydrologically, it is connected to the Rio Piedras Watershed and to the San Juan Bay Estuary, as demonstrated in Figure 1 [28]. Receiving inflow not only from diffuse rainwater discharge but also from multiple smaller tributaries draining upstream areas, water is channeled out of the reservoir through a 'morning glory' concrete pipe located in the northwest, close to middle station 1 [23,28]. The reservoir had an original capacity of approximately 1,381,000 m^3 [26]. Cupey ward hosts a population of 32,833, averaging 4375.7 individuals per square mile [29]. The reservoir basin lacks a public sewage collection system; thus, septic tanks are used for household wastewater disposal [28]. From October 2017 to September 2019, the reservoir had an average phosphorus concentration of 0.05 mg L^{-1}, which increased to 0.10 mg L^{-1} between October 2019 and September 2021; both levels categorize the reservoir as eutrophic [30]. The drainage basin of the reservoir is approximately 2.85 km^2 and land use consists of evergreen forest (43%), grassland (36%), developed (12%), open water (5%), and open space (4%) [28]. The mean annual rainfall in the watershed is approximately 1632 mm, with the rainy season occurring from July to October, and the mean annual temperature for San Juan and Río Piedras is 25.9 °C and 25.7 °C, respectively [31].

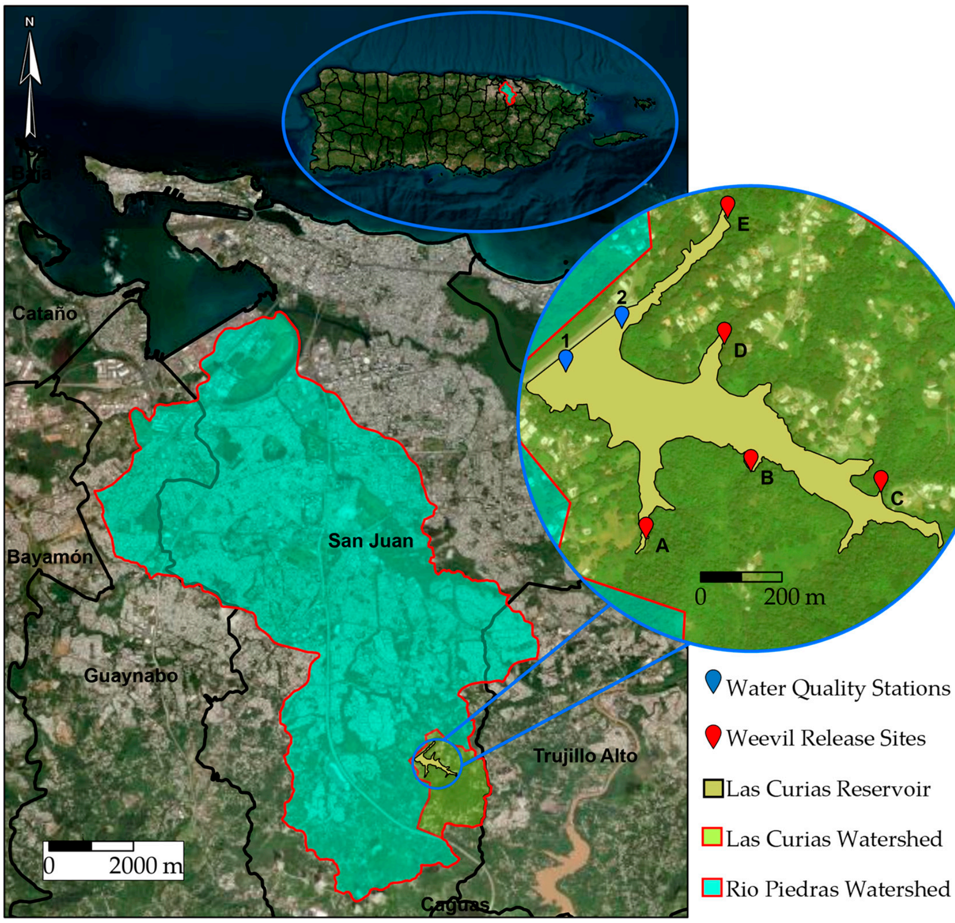

Figure 1. This hierarchical map illustrates the Las Curias Reservoir situated in Cupey, San Juan, Puerto Rico, encompassed by distinct geographical contexts: the Caribbean Island of Puerto Rico, the Río Piedras, and the Las Curias Watershed. Here, we highlight the designated weevil release sites and water quality stations within the limits of the reservoir.

Following introduction of the weevils in September 2019, environmental variables were sampled periodically to quantify changes in salvinia cover and quality, weevil density, and water quality through September 2022. In addition to biological control, an aquatic harvester was brought to the reservoir in October 2019 for mechanical extraction of salvinia; thus, both the mechanical and biological control efforts occurred simultaneously. The aquatic harvester (2017 Weedoo TC Diesel with Quick-Change Skimmer Bucket) was operated, on average, four days per week from arrival until October 2020 when the salvinia mat was too thin to collect. Near the dam and morning-glory spillway, salvinia was deposited onto *R. holoschoenoides* islands in the water, sinking under its own weight when intertwined. Additionally, a significant portion of salvinia was extracted and removed from the reservoir entirely.

2.2. Salvinia Performance

Four flights with an unmanned aerial system (hereafter referred to as a drone) allowed the estimation of salvinia cover in Las Curias. Flights occurred during July 2019, March 2020, January 2021, and August 2022. The flight plan included two flight lines passing over the study area in a north–south direction and a west–east direction. The flight line consisted of 80% photo overlap and 70% flight line overlap at an altitude of about 65 m.

In October 2022, post-salvinia management, the reservoir's depth profiles were measured using the DepthTrax 1H from Hawkeye. To calculate the reservoir's water storage capacity, we followed a standard bathymetric procedure [32,33]. Briefly, we calculated the cross-sectional average area between two adjacent cross-sections and then multiplied this average by the distance between them. The resulting product was the volume for that segment of the reservoir between the adjacent transects. This process was repeated for all cross-sections. Lastly, we summed the volumes to calculate the total reservoir water storage capacity. We used Esri software to transform drone-captured imagery of the Las Curias reservoir surface into maps, produce a detailed representation of the study area, and create a bathymetric map. Specifically, we employed ArcGIS Pro 2.5 (2020), ArcGIS Pro 2.8.4 (2022), ArcGIS Pro 3.1.3 (2023), Drone2Map 2.1 (2021), and ArcGIS Field Maps 22.1.0 (2022) for these tasks.

To characterize the physical condition of the salvinia, mat thickness, and normalized difference vegetative index (NDVI) were sampled. The mat thickness was determined in October 2021 at 15 locations using a plastic tray (0.3×0.4 m), with a string, marked in 1 cm increments, attached to the center of the tray. The tray was slid under the salvinia mat, and was then lifted to measure the thickness. The percentage of green salvinia was estimated visually by placing a quadrant ($0.35 \times 0.21 \times 0.17$ m; [L $\times$ W $\times$ H]; area = 0.01 m^3) in the mat. The normalized difference vegetative index (NDVI) was determined using a handheld Trimble GreenSeeker® (Trimble Agriculture Company, Sunnyvale, CA, USA). The GreenSeeker was held ~1 m above the mat surface and then swept sideways across the salvinia mat for ~1 m. Feeding damage to salvinia caused by weevils (present or absent) and the number of buds with damage were also documented.

2.3. Weevil Introduction and Densities

During September 2019, ~1000 adult weevils were transported from LSU in Baton Rouge, LA, to the UPR-RP. Upon arrival in the laboratory, weevils were transferred to fresh salvinia collected from Las Curias then transported to the reservoir and placed in a protected area (Figure 1, initial inoculation arm D). The weevils were first released in six floating fine meshed cages filled with salvinia. This was carried out to increase the likelihood of weevils encountering one another and thus increase the probability of reproduction. After two months, browning of salvinia in the cages indicated the presence of larvae. At this time, half of the salvinia in the cages were removed and placed within the mat outside of the cages. Fresh salvinia from the lake was placed back in the cages to promote further reproduction. This was repeated for six months until the cages degraded, and the weevils naturally escaped to nearby locations.

In June 2020, weevil establishment was assessed by measuring densities within arm D. In December 2020, weevils had exceeded the density of ~40 adults per kg of wet salvinia recommended for transfer [34,35]. Salvinia infested with weevils was transported from the inoculation site to arms A, B, C, and E (Figure 1). Salvinia samples were collected from the sampling stations on various dates between 2020 and 2022. These samples were used to quantify weevil densities across the different stations and sampling dates. The specific sampling dates were 6 June 2020, 7 and 20 December 2020, 17 and 21 May 2021, 10 October 2021, 18 February 2022, and 14 July 2022. During each monitoring event, approximately 200 to 500 g of salvinia were collected near the sampling stations using a dip net. This amount of salvinia was collected to remove as few weevils as possible from the lake while still being able to determine density changes. Samples were placed in resealable plastic bags then transported to the laboratory for Berlese funnel extraction. The wet mass of each salvinia sample was recorded prior to being placed inside the Berlese funnels [36]. Salvinia was placed in the funnels for 48 h, and escaping adults and larvae were collected in 95% ethanol, then counted.

2.4. Water Quality

Physicochemical water quality parameters were collected from two stations during 19 sampling occasions from September 2019 to September 2022 (Figure 1). A Hydrolab MS5 Multiparametric sonde measured specific conductance (µS/cm), dissolved oxygen (DO; mg L^{-1}), pH (s.u.), and temperature (°C) at fixed depths intervals in the water column. The instrument was calibrated before each sampling event to ensure the accuracy of the measurements. Due to a sensor malfunction, no specific conductance data were collected during the December 2020 and March 2021 sampling events. A Secchi disk was used to measure water transparency and to estimate the depth of the photic zone. Additionally, an Onset UA-002-08 HOBO Pendant Data Logger rain gauge was installed to continuously track rainfall over the study period.

2.5. Statistical Analysis

To assess the internal reservoir dynamics, physicochemical water quality parameters were analyzed throughout the years within a water column depth zone (epilimnion, thermocline, and hypolimnion). The location of the zones was determined by observing in situ variations in specific conductance for each sampling date. While the epilimnion was generally found in the upper two meters and the hypolimnion below six meters with a thermocline in between, for the analyses, we defined the epilimnion zone as 0–2 m depth, the thermocline as 3–5 m, and the hypolimnion as >5 m. We combined data from both stations for statistical analyses. Statistical analyses were conducted using R and Python statistical software. Specifically, version 4.1.2 "Bird Hippie" (2021) and version 4.3.1 "Beagle Scouts" of R software were employed as well as Python version 3.10.12 (2023). Linear models were developed to examine the differences in specific conductance and temperature between depth zones, years, and the interaction of depth zone with year. A linear model was examined to determine the differences in dissolved oxygen in the epilimnion between years, but no statistical analyses were calculated for thermocline or hypolimnion due to the overabundance of zero values. A Gamma-distribution, log-link function generalized linear model (GLM) was used to examine the differences in pH between depth zones, years, and the interaction of depth zone with year. Secchi depths from both stations were combined to calculate the mean depth of the photic zone as an index of ecosystem recovery.

3. Results

3.1. Salvinia Performance

In summer 2019, salvinia covered the entire reservoir at 100% (17.7 ha); Figures 2a and 3a). Aquatic and terrestrial plants such as *Rhynchospora holoschoenoides*, *Mikania* sp., *Pistia stratiotes*, and *Hydrocotyle* sp., colonized the large salvinia mat, growing amongst the floating plant material (Figure 2a). It was not practical to distinguish among plants on the surface; thus, we defined any visible coverage as salvinia, since it was the base for other plants. By March 2020, biological and mechanical control methods had been in place for approximately six months and salvinia coverage decreased by 17%, resulting in an estimated coverage of 83% (14.7 ha; Figure 3b). By January 2021, the salvinia coverage had been reduced by 71%, leaving a remaining coverage of 29% (5.1 ha), with the plant being concentrated in the arms of the reservoir (Figure 3c). As part of the mechanical control strategy, vegetative islands *R. holoschoenoides* growing on top of decomposing salvinia were pushed to the bottom of station E during the summer of 2022. The salvinia coverage was further reduced by 94% in August 2022, representing a 6% coverage (1.1 ha) (Figure 3d). As open water areas expanded, salvinia and other organic materials sunk, altering the depth. Using our multiparametric sonde to measure physicochemical parameters at station 1, we observed the instrument reaching the bottom at shallower depths, indicating a change from 19 m in September 2019 to 7 m in September 2021. This suggests an approximate 12 m accumulation of biomass on the reservoir floor. Following these changes, the calculated volume (nominal capacity) of the reservoir was 769,157 m^3 (Figure 4). A field survey in October 2021 showed that the mean wet weight of salvinia extracted from the quadrant was 165.6 g (±113.4 [±SE], n = 15), and the mean dry weight was 9.3 g (±6.9, n = 15). Mat thickness was 1.3 cm (±0.9, n = 15), mean percent green was 40% (±25.6, n = 15), and mean NDVI was 0.5 (±0.1, n = 15). As open water areas expanded, salvinia and other organic materials sunk, altering the depth (Figure 2b).

Figure 2. Aerial imagery captured by drone reveals the variations in plant coverage within Las Curias Reservoir, Puerto Rico, between September 2019 ((**a**), above) and October 2021 ((**b**), below). These comparative visuals underline the evolution of vegetative cover, providing a distinct perspective on the salvinia removal efforts over the course of the study period.

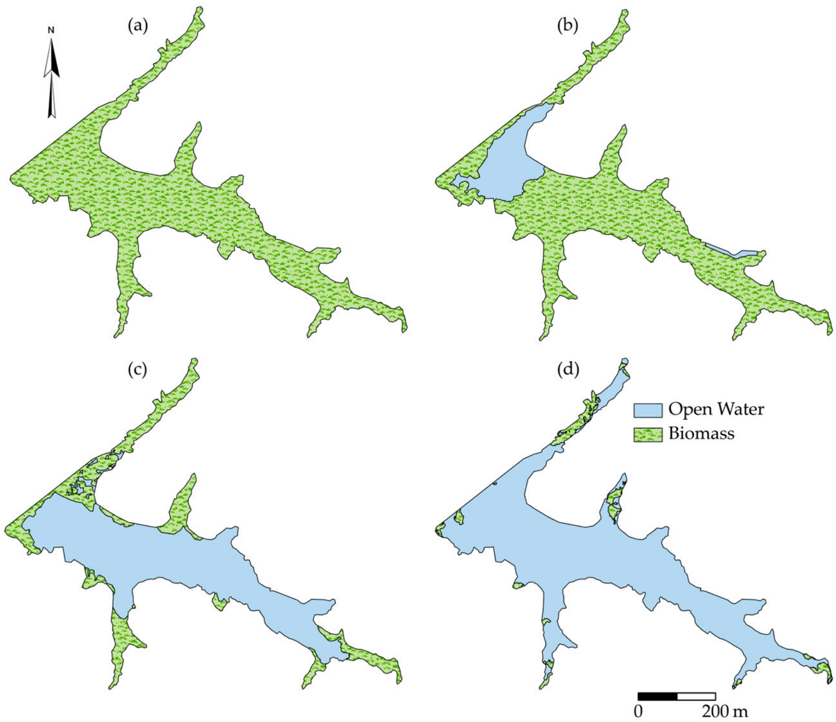

Figure 3. The series of maps illustrates the reservoir's transformation over time, highlighting the reduction biomass coverage dominated by salvinia: from an initial 100% coverage on 23 July 2019 (**a**), to 83% by 7 March 2020 (**b**), further decreasing to 29% by 29 January 2021 (**c**), and a stark decline to just 6% by 12 August 2022 (**d**). The green areas on each map represent biomass, while the blue sections denote water regions free from aquatic plants.

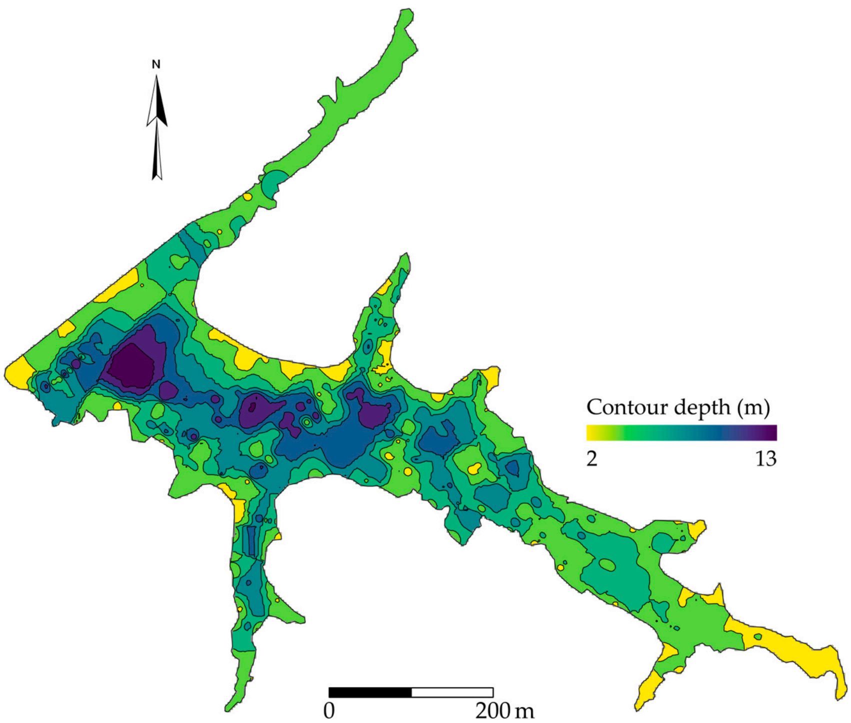

Figure 4. Bathymetric map of Las Curias Reservoir developed in October 2022 illustrating underwater topography variations. Lighter shades (from yellow to green) signify shallower areas, while darker blues denote deeper regions. Contour depths are relative to a spillway crest elevation of 96.3 m above mean sea level (amsl).

3.2. Weevil Performance

Periodic monitoring of weevil densities was conducted from initial release through July 2022 (Figure 5). In June 2020, initial surveys found that 49 of 189 buds sampled from arm D had visible feeding scars, and the mean weevil density was 19.2 (SE = 11.7) adults per kg of wet salvinia. In December 2020, 198 of 1364 buds inspected between stations B and C showed visible damage, while the overall mean weevil density for the month was 50.8 (SE = 18.5). After this date, weevils were transported and released to other arms of the reservoir. Approximately five months after transport, weevils were established at each of the release sites (Figure 5), and the mean weevil density across all arms was 43.1 (SE = 14.2). Due to management efforts, the presence of salvinia in the reservoir was reduced and the previous weevil sampling locations no longer had floating vegetation. In October 2021, the salvinia cover had been reduced to only three arms, and 69 out of 150 inspected buds had weevil damage, with a mean density of 68.6 (SE = 30.5) weevils per kg in the reservoir. By July 2022, only two arms contained salvinia at a mean density of 34.1 (SE = 10.5) weevils per kg, and sampling ceased as the salvinia cover was <10%.

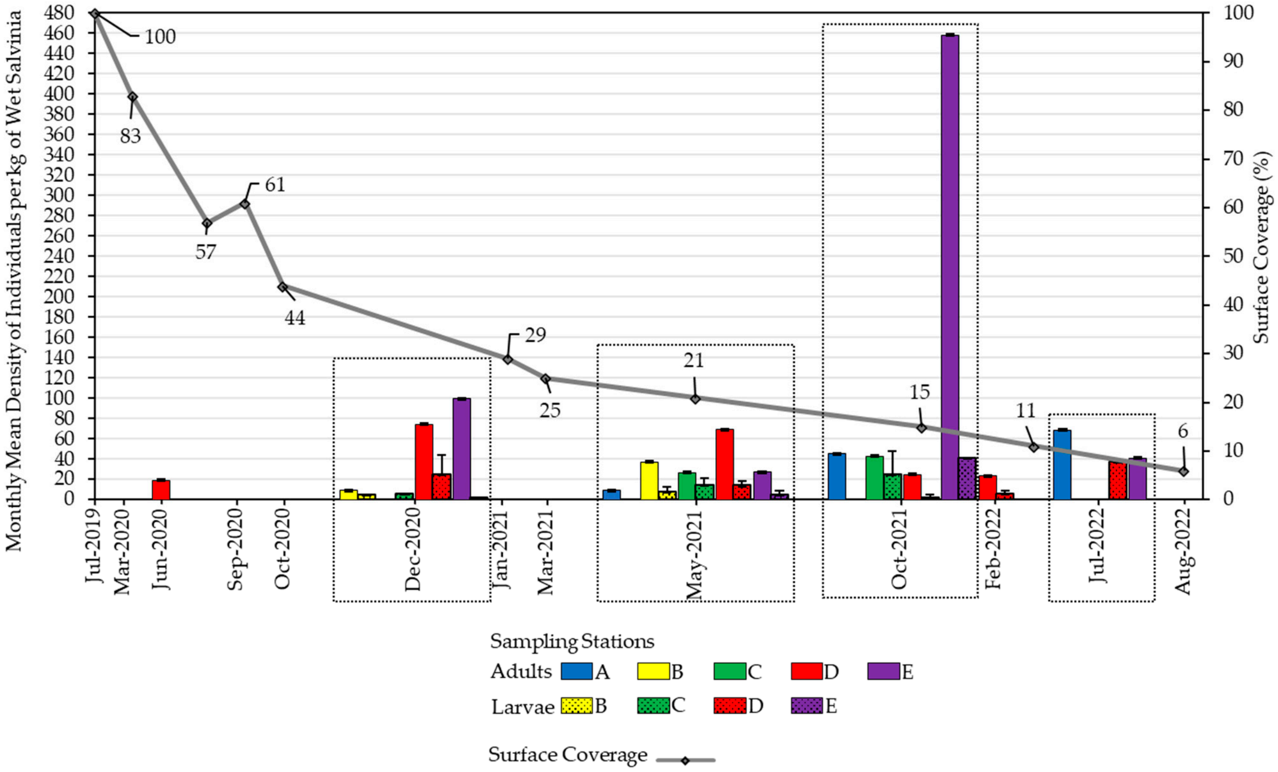

Figure 5. Depiction of *Cyrtobagous salviniae* (weevil) adult and larval densities along with salvinia coverage in Las Curias Reservoir from July 2019 through August 2022. The graph presents specific months during which drone flights and weevil density monitoring were conducted. The gray scatter plot line donates salvinia surface coverage. Solid colored bars represent mean densities of *C. salviniae* adults per kg of wet salvinia across stations, while solid bars with dots represent the same for larvae. Whiskers indicate the associated standard error. The softly outlined rectangles group data collected within the same month.

3.3. Water Quality

Specific conductance differed by depth zones (f = 34.18, df = 2, $p < 0.001$), years (f = 64.79, df = 3, $p < 0.001$), and their interaction (f = 4.38, df = 6, $p < 0.001$; Table 1). In 2019, the epilimnion and hypolimnion specific conductance (178–226 µS/cm) was about 42% lower than in subsequent years (283–344 µS/cm). The 2021 thermocline specific conductance surpassed the other years by at least 10%. Overall, the specific conductance rose from 2019 to 2022, with minor declines after rain events in February and September 2022 (Figure 6a).

Dissolved oxygen (DO) in the epilimnion rose over three years post-management actions (Table 1; Figure 6b). Rain in August 2020 and September 2022 notably reduced DO, whereas February 2022 rain boosted it. Yearly DO variations were significant (f = 11.504, df = 3, p-value < 0.001), with 2022's mean (5.4 mg L^{-1}; SE = 0.4) surpassing prior years. From summer 2020, DO penetrated the thermocline, yet 78% of readings were below 1 mg L^{-1}, and all hypolimnion measurements fell beneath this due to decomposing salvinia.

pH rose across all water layers (Table 1; Figure 6c). Depth zone, year, and their interaction influenced pH levels significantly. In 2022, the epilimnion pH increased by approximately 1.20 units from its earlier value in 2019, and the hypolimnion pH increased by roughly 0.54 units from its 2019 level. In 2021, the thermocline pH was higher by 0.41 units compared to its 2019 value, and it decreased by 0.39 units in 2022 from the previous year.

Table 1. Mean values (±SE) of water quality variables recorded in Las Curias Reservoir, from September 2019 to September 2022. Data represent the combined results from two sampling stations. Depth zones are categorized as: epilimnion (0–2 m depth), thermocline (3–5 m depth), and hypolimnion (>5 m depth).

Depth Zone	Year	Specific Conductance (μS/cm)		Dissolved Oxygen (mg L^{-1})		pH		Water Temperature (°C)	
		N	Mean (±SE)	N	Mean (±SE)	N	Mean (±SE) (Range)	N	Mean (±SE)
Epilimnion	2019	6	178.4 (±15.4) [a]	6	1.7 (±1.2) [a]	6	6.53 (±0.08) [a] (6.34–6.8)	6	25.8 (±0.4) [a]
	2020	18	285.7 (±2.0) [b]	24	3.4 (±0.4) [a]	24	6.72 (±0.03) [a] (6.47–6.96)	24	28.5 (±0.3) [b]
	2021	24	282.6 (±2.9) [b]	30	2.8 (±0.3) [a]	30	6.91 (±0.04) [a] (6.51–7.29)	30	27.8 (±0.2) [b]
	2022	54	291.8 (±3.9) [b]	54	5.4 (±0.4) [b]	54	7.73 (±0.06) [b] (7.01–8.41)	54	28.2 (±0.2) [b]
Thermocline	2019	6	212.6 (±0.4) [b]	6	0.0 (±0.0)	6	6.43 (±0.03) [a] (6.35–6.51)	6	23.9 (±0.1) [a]
	2020	18	272.4 (±5.7) [b]	24	0.3 (±0.1)	24	6.40 (±0.03) [a] (6.09–6.6)	24	26.7 (±0.2) [b]
	2021	24	325.5 (±4.5) [c]	30	0.9 (±0.3)	30	6.84 (±0.05) [b] (6.27–7.5)	30	26.9 (±0.1) [b]
	2022	53	295.3 (±5.7) [b]	53	1.0 (±0.2)	53	7.23 (±0.04) [c] (6.76–7.96)	53	27.1 (±0.2) [a]
Hypolimnion	2019	17	225.9 (±3.8) [a]	17	0.0 (±0.00)	17	6.43 (±0.01) [a] (6.36–6.49)	17	23.5 (±0.0) [a]
	2020	27	344.3 (±7.3) [b]	36	0.0 (±0.00)	36	6.19 (±0.02) [a] (5.97–6.46)	36	24.9 (±0.1) [b]
	2021	17	331.0 (±4.8) [b]	24	0.1 (±0.01)	24	6.57 (±0.05) [ab] (6.15–6.95)	24	26.1 (±0.1) [c]
	2022	37	322.1 (±11.8) [b]	37	0.0 (±0.01)	37	6.97 (±0.05) [b] (6.24–7.63)	37	25.5 (±0.2) [bc]

Note: "N" denotes the number of observations for each year and depth zone. Statistical differences within a depth zone across years are indicated by superscript letters; for instance, values marked with "[a]" are significantly different from those marked with "[b]", and so forth.

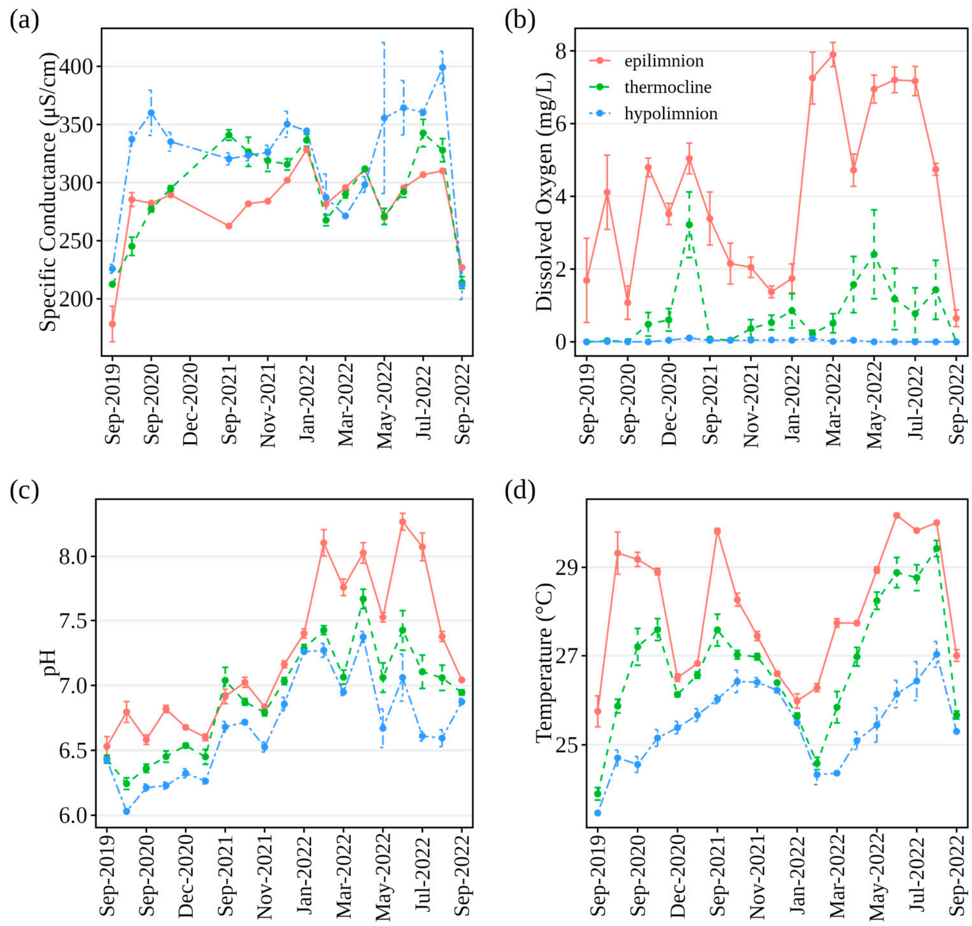

Figure 6. Water quality trends in Las Curias Reservoir from September 2019 to September 2022. Panels show (**a**) specific conductance, (**b**) dissolved oxygen, (**c**) pH, and (**d**) temperature. Data, grouped by depth zones (epilimnion ≤ 2 m, thermocline 3–5 m, hypolimnion > 5 m), combines all sampling stations. Points depict mean value with standard error bars.

Las Curias displayed marked thermal stratification, peaking at a 5.7 °C gradient in September 2020 (Figure 6d). This gradient shrank to 1.4 °C during winter (December 2021–January 2022). Significant rainfall, like February 2022's 240 mm in three days (Figure 7), mixed waters, disrupting stratification. Temperature differed based on depth zones, years, and their interplay (Table 1). The epilimnion's 2019 mean temperature was 7% cooler than in subsequent years. Thermocline temperatures in 2019 lagged by at least 7% compared to 2020 and 2021 but dropped by 15% from 2021 to 2022. The 2021 hypolimnion temperatures surged by 11% when compared to 2019 or 2020.

As shown in Figure 7, light penetration in the reservoir, as measured by the Secchi depth, generally improved over the study period. This improvement is consistent with the previously discussed reduction in salvinia coverage. In 2019, the average Secchi depth was a mere 0.1 m, but by August 2022, it had increased significantly to a maximum of 2.23 m. Particularly, the Secchi depth exhibited declines after notable rain events, such as those in July 2020 and September 2022. Storm Isaias, which transpired from 29 to 31 July 2020, led to rain accumulations of 152.4 to 254 mm [37]. Similarly, Hurricane Fiona, which occurred from 18 to 21 September 2022, resulted in rainfalls of 202 to 380 mm [38]. These events likely caused the observed reductions in Secchi depth due to increases in suspended sediment loads.

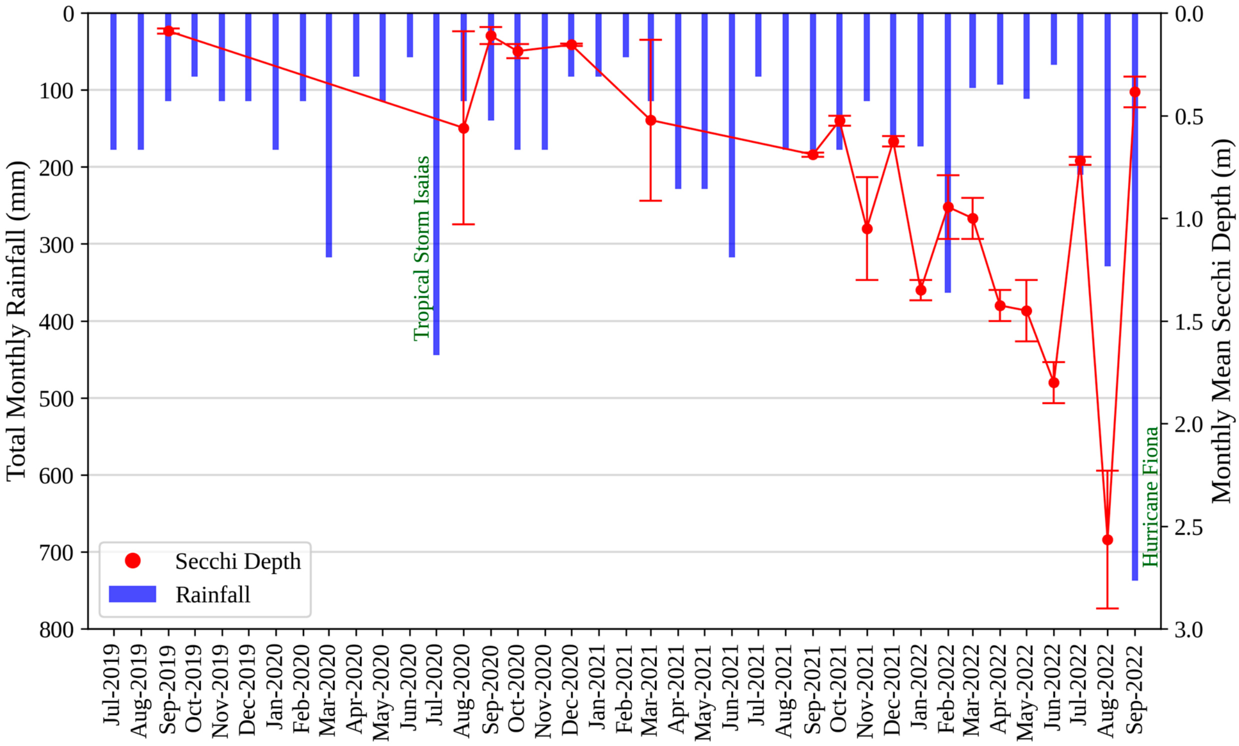

Figure 7. Mean Secchi depth (m) with standard error bars in red and total monthly rainfall (mm) in blue at Las Curias Reservoir from July 2019 to September 2022. Rainfall data for July 2019–November 2021 were sourced from the National Weather Service's Advanced Hydrologic Prediction [39] while data from December 2021 to September 2022 were from a gauge near the Las Curias dam. Events such as Tropical Storm Isaias (July 2020) and Hurricane Fiona (September 2022) are highlighted in green due to their significant rainfall impact.

4. Discussion

The proliferation of invasive species can reduce ecosystem stability via shifting environmental conditions, often displacing native taxa, reducing biodiversity, and requiring costly management efforts to control the invader and restore ecological conditions [40–42]. Mitigating effects from invasive species is a daunting task and determining when a system has completely recovered can be challenging as well. Environmental variables may respond unproportionally to control efforts, potentially taking years or decades until natural state conditions return [43,44]. Therefore, knowledge about how different aspects of the environment rebound following control could be beneficial for setting realistic restoration goals [45]. Spatially isolated invasions provide a practical system for tracking the recovery of environmental quality, as localized management efforts could be more impactful, and the lack of colonist sources will limit reinvasion following initial control. In this study, we quantified recovery in a tropical lentic ecosystem following the implementation of biological and mechanical control efforts to remove an invasive aquatic species. We found that environmental variables recovered differently and the degree to which variables recovered varied throughout the water column.

As we predicted, the warm temperatures and longer growing season of Puerto Rico allowed the weevil to establish, grow, and ultimately control salvinia. This success is similar to biological control programs implemented in tropical and subtropical regions of United States, South Africa, Senegal, and Australia [17,46–50]. The air temperatures of Las Curias fluctuate between 23 and 30 °C during winter and summer, respectively, matching near perfect conditions for the weevil's adult feeding, dispersal (flight and walking), reproduction (mating, oviposition), and larval development [51–54]. Additionally, anthropogenic, and internal nutrient sources to the reservoir [23,28] most likely resulted in salvinia with a high nitrogen concentration in the buds, which has been known to increase weevil reproduction [51]. We speculate that these factors led to an optimal scenario not only for population growth of weevils but also their rapid dispersal and colonization of salvinia across the entire reservoir (Figure 5). Salvinia damage by the weevil was noticeable at different scales from reduction of NDVI, feeding holes of leaves, yellowing, and browning of plants, to sinking of entire floating mats. Our quadrat data on salvinia density showed a drastic reduction in growth rates of the plant following the release of the weevil. This makes us wonder about a weevil density at which there is a point of no recovery of salvinia, or a putatively tipping point where the damage is so severe that salvinia collapsed and sunk. Future studies should aim to understand the relationship among weevil densities, nutrient load, and growth rates of salvinia [17]. Finally, sampling towards the end of the project (2022) revealed that weevils did not extirpate salvinia from the reservoir, but rather weevils and salvinia reached an equilibrium at lower densities. We can speculate that this ideal equilibrium of the salvinia–weevil system could be easily altered by external disturbances, and therefore should be monitored.

Water quality variables were in various stages of recovery following salvinia control. Specific conductance increased following the sinking of salvinia, and the highest values were recorded in the hypolimnion, representing plant decomposition on the lake bottom and probable nutrient release from the sediment [55,56]. Mean specific conductance in the reservoir ranged from 250–280 μS/cm from 2014–2017 [23], and specific conductance in the epilimnion at the end of the study (mean = 291 μS/cm; SE = 4) was near pre-salvinia invasion levels. In the four years prior to salvinia invasion, the mean pH in the reservoir ranged from 7.24–7.93 [23]. After the control efforts, the pH in the epilimnion (mean = 7.73; SE = 0.05) and thermocline (mean = 7.22; SE = 0.04) returned to pre-invasion conditions, while the hypolimnion remains slightly acidic (mean = 6.96; SE = 0.05), suggesting salvinia plant matter remains on the lake bottom. Salvinia prefers a slightly acidic environment [57] and creates these conditions when covering large portions of the water surface. Mean surface water dissolved oxygen ranged from 4.0–6.9 mg L^{-1} in the years prior to salvinia invasion [23]. By September 2022, the dissolved oxygen in the epilimnion returned to pre-invasion levels and was permeating into the thermocline, while the hypolimnion remained anoxic. The recovery of pH and DO in the epilimnion following three years of management efforts demonstrates the resiliency of ecosystems with regard to returning to a natural state once the disturbance is removed; however, more time is needed to recover water quality through the entire waterbody. The lack of DO and the acidification of deeper depths creates conditions for sedimentary nutrient release and internal loading of phosphorus [58,59]. Nutrients released from decomposing litter can contribute to future eutrophication and proliferation of aquatic invasives in the reservoir [60].

We predicted that the reduction in salvinia coverage would accelerate the rise in epilimnetic water temperature, dissolved oxygen, pH, and specific conductance, subsequently improving water transparency. This prediction was contextualized by the significant salvinia biomass estimated at 3449 metric tons in 2019 [23], a substantial portion of which eventually settled at the bottom of the reservoir. This extensive biomass accumulation also resulted in a 44.3% reduction in the reservoir nominal water storage capacity compared to the original design capacity of 1.4 million cubic meters (Mm^3). By October 2021, data revealed a 20.7 cm reduction in the thickness of the salvinia mat, a 27% decrease in the percent green, and a 0.02 diminution in NDVI, relative to the 2019 measurements [23]. The aftermath of such biomass accumulation impacted the reservoir's oxygen levels, particularly below the epilimnion, where dissolved oxygen was virtually absent, being consumed faster than it could be replenished owing to decomposition processes. This led to a scenario where, due to the rapid oxygen depletion in the hypolimnion, microbial respiration transitioned to anaerobic pathways, fostering redox stratification (i.e., the water column became stratified in terms of the distribution and speciation of redox-sensitive elements) [61–63]. During our observations, dense black mats of decomposing salvinia surfaced after initially sinking, propelled by gas production. It is probable that the salvinia decomposed anaerobically at the bottom, but upon rising to the surface, continued to decompose aerobically. Decomposition of salvinia in anaerobic conditions results in the release of carbon dioxide and methane [64,65]. The input of organic carbon, such as plant matter, to anaerobic sediments significantly augments methane production in reservoirs, turning any system with anoxic conditions and high sedimentation rates into potential methane emitters [66]. Given the volume of sunk biomass and the relatively slow decomposition rate of salvinia tissue, Las Curias could potentially be a source of methane emissions.

The pronounced thermal stratification observed in Las Curias on most sampling dates was atypical for Puerto Rican reservoirs, as indicated by Gustavo Martinez (personal communication) [67]. The warm waters of tropical lakes are less viscous than their temperate counterparts and, therefore, are more susceptible to mixing due to winds and surface cooling by rain [68]. Thus, seasonal changes in precipitation and thermal regimes in tropical lakes are important driving factors for stratification and mixing [69,70]. The absence of strong seasonal temperature fluctuations precludes seasonal convective overturn as a mechanism to transport oxygen into deep waters [71]. Complex vertical profiles were also documented in the La Plata reservoir in Puerto Rico, due to the combination of stratification plus inflow created by the sinking of turbid and oxygenated storm runoff within this tropical reservoir [72]. Mixing patterns through the reservoir are influenced by the depth at which water is released from the dam. Since Las Curias is not used as a municipal water source anymore, vertical mixing is entirely driven by environmental conditions. When a high density of salvinia was present, the hypolimnion appeared at four meters depth, with a maximum thickness of 15 m near the dam. Las Curias was stratified most of the year, with anoxic conditions throughout the hypolimnion. Temperature decreases were observed in the entire water column in December 2020, and February 2022 and September 2022 (Figure 6d), indicating that mixing events occurred in Las Curias. Drops in temperature in the water column may be representative of mixing events and the direct effect of controlling and removing salvinia from the water surface. The significant rise in Secchi depth throughout the study suggests a shift in aquatic ecosystem dynamics. Reduced salvinia coverage undoubtedly boosted water transparency, and the possible return of submerged macrophytes. Filtering of particles by submerged macrophytes and competition with phytoplankton could further enhance clarity [18,73]. This interplay between macrophytes, phytoplankton, and external factors like rain events reflects the complex nature of aquatic ecosystems, consistent with prior research conducted in Lake Kariba the largest manmade African lake [74].

Our results corroborated our prediction that the combination of mechanical and biological control led to a rapid reduction in salvinia coverage. By late 2020, the weed harvester was no longer needed, since the salvinia growth was nil and weevil damage was widespread. Weevil densities were routinely above 40 individuals per kg from December 2020 through the end of the study, suggesting that biological control reached an equilibrium at lower weed densities where additional control measures are no longer needed [75]. As salvinia decreased, water quality began to recover, with general increases in specific conductance, DO in the epilimnion, pH, water temperature, and light penetration. Tracking the recovery of water quality following salvinia is not well documented in the tropical literature, and this case study provides a great opportunity to quantify recovery after removal. Monitoring should continue to track the recovery of the system and protect against future invasions. To secure the access to salvinia weevils, we recommend establishing populations in other locations in Puerto Rico infested with salvinia. Disturbance events in the reservoir could result in the localized extinction of the weevil, and if salvinia were to recolonize, additional weevils could be collected from other release locations. As salvinia coverage decreased, water quality began to recover, with general increases in specific conductance, DO in the epilimnion, pH, water temperature, and light penetration. Massive salvinia biomass accumulation on the reservoir bottom, along with internal nutrient loading through organic matter decomposition and sedimentary release, creates ideal conditions for the re-invasion of other aquatic plants or the onset of algal blooms. Establishing a long-term monitoring program for Las Curias is critical to track the recovery of the system and provide protection against future invasions.

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