J. Aquat. Plant Manage. 61: 42–54

Biological control of invasive floating fern leads to rapid recovery of ecological functions in coastal freshwater wetlands in Louisiana

STEVEN E. WOODLEY, CHARLES F. WAHL, ALEXANDER TRYFOROS, AND RODRIGO DIAZ*

ABSTRACT

Despite the success of the salvinia weevil (*Cyrtobagous salviniae*) at controlling giant salvinia (*Salvinia molesta*), its impact on the timing of reduction of giant salvinia cover and recovery of submerged aquatic vegetation (SAV) and dissolved oxygen remains unknown. A two-year field study (2016 to 2017) was conducted in coastal wetlands in southwestern Louisiana to measure the impact of biological control of giant salvinia. Water temperature, dissolved oxygen, weevil densities, and giant salvinia and SAV cover were assessed at 36 sampling locations comprising canals, small ponds, and large ponds. Results showed that adult weevils were distributed across the landscape. In 2016 mean adult densities were 46.9 weevils kg^{-1} in canals, 42.5 weevils kg^{-1} in small ponds, and 38.7 weevils kg^{-1} in large ponds. In 2017 mean adult weevil densities were 28.2 kg^{-1} in canals, 12.3 kg^{-1} in small ponds, and 29.4 kg^{-1} in large ponds. Percent cover of SAV was zero at all three site types in July 2016 but increased by 29.4, 35.0, and 73.3% in small ponds, canals, and large ponds, respectively, from July 2016 to January 2017. Our models demonstrate that higher adult weevil densities in June lead to faster control of giant salvinia and SAV recovery, subsequently increasing dissolved oxygen levels. The models can be used to estimate months needed to control salvinia given weevil density, percent salvinia cover, and site type. Resource managers could apply this to inform about timing to control and guide management decisions.

Key words: *Cyrtobagous salviniae*, dissolved oxygen, invasive species, *Salvinia molesta*, wetland restoration.

INTRODUCTION

Half of the wetland acreage has been lost since 1900 in the contiguous United States (Mitsch and Gosselink 2000), including 80% only in Louisiana (Williams 1995). Despite this loss, Louisiana's wetlands encompass about 40% of the wetlands in the United States, which extends 130 km inland and 300 km along the coast (Williams 1995). Coastal freshwater wetlands in Louisiana are essential habitats for fish and wildlife and provide various recreational opportunities such as hunting, fishing, and bird watching, which are important economic revenues for the state (Barnes et al. 2015). It is estimated that waterfowl hunting alone generates $110 million annually in Louisiana (Barnes et al. 2015). However, many of the wetlands remaining in Louisiana are losing their essential functions and ecosystem services due to aquatic weeds.

One of the worst aquatic weeds in Louisiana is giant salvinia (*Salvinia molesta* Mitchell) (Salviniales: Salviniaceae). Giant salvinia was first discovered in Louisiana in 1998 in the Toledo Bend Reservoir (Jacono 1999) and since then has invaded many of the waterbodies throughout the state. The spread of giant salvinia is attributed to its rapid growth and ability to reproduce asexually from rhizomes and plant fragments (Thomas and Room 1986; Room 1990; Oliver 1993; McFarland et al. 2004). Giant salvinia can double its biomass within three days under favorable conditions (Barrett 1989; Johnson et al. 2010) and can cover an entire waterbody in a dense floating mat up to 1 m thick when left unmanaged (Thomas and Room 1986). Thick salvinia mats restrict sunlight penetration resulting in suppression of submersed aquatic vegetation (SAV) (Netten et al. 2010), which is an important source of food and habitat for fish, waterfowl, and invertebrates (Poirrier et al. 2010; Van Driesche et al. 2010). The loss of SAVs reduces dissolved oxygen levels, which can cause localized die-offs or emigration of fish and wildlife (Chapman and Kimstach 1996; Flores and Carlson 2006). Consequently, thick mats of giant salvinia restrict commercial and recreational opportunities (McFarland et al. 2004), such as fishing and waterfowl hunting, leading to a loss in economic revenues.

A successful tool to manage giant salvinia in subtropical and tropical regions is the biological control agent salvinia weevil (*Cyrtobagous salviniae* Calder and Sands) (Coleoptera: Curculionidae) (Room and Kerr 1983; Thomas and Room 1986; Cilliers 1991). Native to southeastern Brazil, Paraguay, and northern Argentina (Calder and Sands 1985; Wibmer and O'Brien 1986), the salvinia weevil was introduced to the United States in 2001, initially in Louisiana and Texas (Tipping 2004; Tipping et al. 2008). Salvinia weevil adults average 2.5 mm in length and feed on the buds and fronds of giant salvinia (Johnson et al. 2010; Knutson and Mukherjee 2012). However, most damage is caused by the salvinia weevil larvae, which burrow into the stem or petiole

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*First author: Postdoctoral Research Associate, School of the Environment, Washington State University, Pullman, WA 99164; Second author: Department of Biology, University of North Carolina Greensboro, Greensboro, NC 27412; Third author: Data Scientist, GoGuardian, Brevard, NC 28712; Fourth author: Associate Professor, Department of Entomology, Louisiana State University, 404 Life Science Building, Baton Rouge, LA 70803. Corresponding author's e-mail: steven.woodley@wsu.edu. Received for publication 09/08/2022 and revised form 05/16/2023.

DOI: 10.57257/JAPM-D-22-00011

and tunnel into plant tissue with higher nitrogen concentrations (Sands et al. 1983). Through the tunneling activity by the larvae, the nutrient uptake of giant salvinia is inhibited, causing the plant to quickly die back and sink (Forno and Harley 1983). In a 400-ha lake infested with giant salvinia in Queensland, Australia, 1,500 adult salvinia weevils were released, and after seven months, the infestation was reduced by 80% (Room et al. 1981). Because of the rapid and long-term control associated with the salvinia weevil, the agent has been released in more than 15 tropical and subtropical countries over the last 40 years (Knutson and Mukherjee 2012; Winston et al. 2022).

The impact of the salvinia weevil has varied in the southern United States based on location, the timing of releases, and annual climatic conditions (Tipping et al. 2008; Obeysekara et al. 2015). Rapid biological control of giant salvinia has been documented in coastal wetlands in Louisiana, wherein biomass was reduced by 99% within two years of the initial salvinia weevil release (Tipping et al. 2008). Despite this success of biological control in subtropical climates, the timing of the reduction of giant salvinia cover remains unknown. Specifically, the need for more aggressive control methods such as herbicides (Mudge et al. 2014, 2016) or lake drawdowns (Cooke et al. 1986; McFarland et al. 2004) depends on the timing of control by the salvinia weevil (Cozad et al. 2019). For example, if plant cover is high at a site and salvinia weevil densities are low, it will likely take a longer time for the insects to control giant salvinia; thus, a more rapid form of control may be desired. As importantly, the timing of the recovery of ecological functions of wetlands following the control of giant salvinia is less understood and includes the reestablishment of SAVs, recovery of macroinvertebrate communities, and subsequent increase of dissolved oxygen levels (Wahl et al. 2021a, 2021b). Additionally, the process of restoring ecosystem state and function to preinvaded conditions during and following biological control is not well documented (Motitsoe et al. 2020a). Thus, providing insight into the timeframe required to recover SAV, restore water quality and chemistry (e.g., improved dissolved oxygen and nutrient reduction), and return invertebrate and fish communities is difficult.

Our overarching goal was to assess the timing of biological control of giant salvinia and wetland recovery. The specific objectives of this research were to 1) examine the distribution of adult salvinia weevil abundance over a large geographic area, 2) measure seasonal population dynamics of adult weevils, plant cover, and water quality, and 3) develop predictive models to estimate the time it takes to reduce giant salvinia cover and increase dissolved oxygen levels.

MATERIALS AND METHODS

Study area

Seasonal trends in adult salvinia weevil densities, giant salvinia cover, SAV cover, water temperature, and dissolved oxygen levels were assessed from June 2016 through November 2017 in a complex of coastal freshwater wetlands covering approximately 8,000 ha in Cameron Parish in southwestern Louisiana. Approximately 10 km from the coastline, wetlands in this area are interconnected and comprised three general *site types*: canals, small ponds, and large ponds. In this study, we refer to a *canal* as an artificial channel, often linear with a degree of flow, connecting small and large ponds. A *small pond* has one point of entry and is $\leq$ 2 ha in water surface area, whereas a *large pond* has more than one point of entry and is $>$ 2 ha in water surface area. Field conditions allowed us to test the following set of predictions: 1) adult salvinia weevil densities will fluctuate across the landscape, 2) sites with higher adult weevil densities reduced giant salvinia cover faster than sites with low densities, 3) dissolved oxygen levels will be higher at sites with lower giant salvinia cover and higher SAV cover, and 4) the earlier giant salvinia is controlled, the faster SAVs will regrow or reestablish and dissolved oxygen levels increase. By monitoring giant salvinia infestations, we were able to construct predictive models estimating the time it takes the weevils to reduce giant salvinia cover and recover desirable dissolved oxygen levels.

The annual mean temperature for the area is 20.2 C (range, 10.6 to 28.2 C), and the total yearly precipitation is 152 cm (PRISM Climate Group 2020) (Supplemental Figure 1). The macroclimate of this region is described as humid subtropical, according to the Köppen-Geiger climate classification, and is characterized by warm temperatures and evenly distributed annual precipitation (Peel et al. 2007). Field monitoring of these wetlands in 2015 suggested a widespread presence of giant salvinia and resident populations of the salvinia weevil. As part of a giant salvinia management program, the salvinia weevil was released in several locations of this property from 2008 to 2014 (C. Courville, property manager, personal communication).

Sampling design

Thirty-six sampling locations were selected based on accessibility and adequate giant salvinia cover. Of the 36 sampling locations, 17 were in canals, nine were in small ponds ($\leq$ 2 ha), and ten were in large ponds ($>$ 2 ha) (Figure 1). Samples were collected once a month in June, July, August, September, and December in 2016 and in January, February, March, May, June, September, and November in 2017.

Five giant salvinia samples were collected around the boat at each sampling location, twice on either side and once in the front. Dissolved oxygen (mg L^{-1}) and water temperature (C) were measured once at a location using a handheld meter[1] at a depth of 20 cm. A $38 \times 24.5 \times 18$ cm (L $\times$ W $\times$ D) quadrat was used to standardize plant biomass for weevil density estimates. Percent giant salvinia and SAV cover were visually estimated across the sampling location. Percent plant cover was visually estimated five times by slowly running three transects with the boat for approximately 200 to 300 m in large ponds or around the entire parameter in canals and small ponds. Typically, giant salvinia could be estimated across the surface of the entire waterbody; however, SAV was estimated within a radius of 2.5 m from the sides of the boat. Species of SAV were noted,

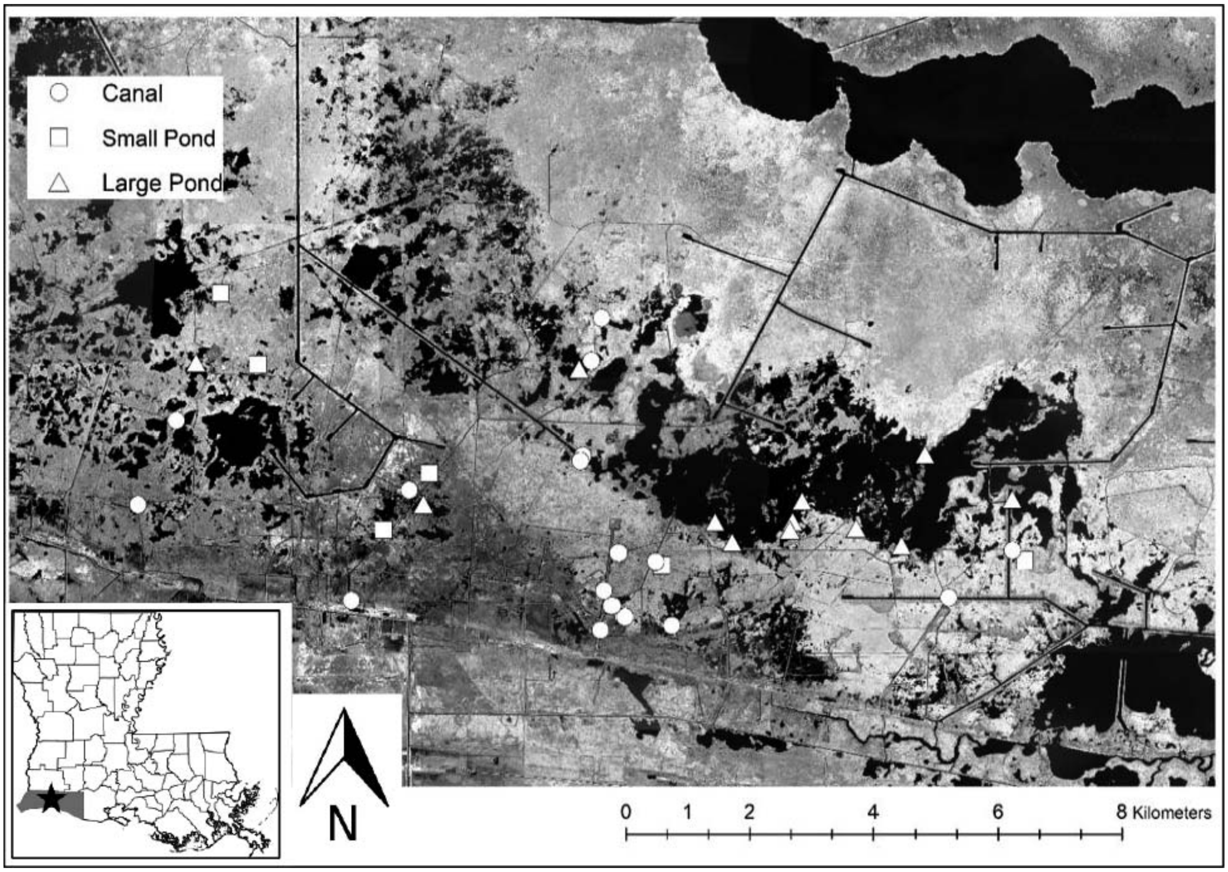

Figure 1. Thirty-six sampling locations comprising canals ($n = 17$), small ponds ≤ 2 ha ($n = 9$), and large ponds > 2 ha ($n = 10$), covering approximately 8,000 ha in Cameron Parish in southwestern Louisiana.

but coverage assessments were not made for each species. Giant salvinia samples were brought back to the lab to assess weevil density. The fresh weight of giant salvinia was determined by draining plants of water for 10 minutes in a bait net[2] before being weighed.[3] To estimate weevil densities, Berlese funnels were used (Boland and Room 1983). Samples were drained and then placed in Berlese funnels for 72 h under 60-watt halogen bulbs to dry. Bags[4] secured to the bottom of the funnels were filled with 80% ethanol to preserve escaping weevils.

Statistical analyses

Trends in weevil dynamics, giant salvinia, SAV, water temperature, and dissolved oxygen levels. Trends in adult weevil densities (number of adults per kg fresh giant salvinia), giant salvinia cover, SAV cover, water temperature, and dissolved oxygen were observed from June 2016 to November 2017 at each of the site types. To assess the distribution of adult weevil densities in June, we grouped the weevil densities into five classes and plotted them in ArcGIS.[5] All analyses were conducted using R statistical software 4.0.0 (R Core Team 2020).

Generalized linear mixed models (GLMMs) were used to examine for differences in giant salvinia cover (Poisson distribution with log link function) and temperature (Gamma distribution with log link function), and liner mixed models (LMMs) were analyzed for differences in dissolved oxygen and SAV cover among site types. Site type and sampling date were fixed effects, and site identification was the random effect in the models. Given a significant result, pairwise comparisons were calculated using estimated marginal means and corrected for multiple comparisons using Tukey's HSD test.

Predicting giant salvinia control. A generalized linear model (GLM), with log link and Poisson distribution, was used to estimate the time it takes to reduce giant salvinia percent cover. The packages used included "caret" (Kuh 2020), "tidyverse" (Wickham et al. 2019), "iml" (Molnar et al. 2018), and "Metrics" (Hamner and Frasco 2018). The dependent variable was a created metric, "time until," used to estimate the time in months it takes, beginning in June until giant salvinia cover fell below 15%. The independent variables for the model were adult weevil densities, giant salvinia percent cover, and site type. The GLM equation to predict the time it takes to reduce giant salvinia percent cover below 15% is shown below:

$$\begin{aligned}\text{Log(time in months)} = {} & \text{intercept} \\ & + [(\beta_0 \times \text{adult weevil densities}) \\ & \quad +(\beta_1 \times \text{giant salvinia cover}) \\ & \quad +(\beta_2 \times \text{site type})].\end{aligned}$$

Giant salvinia cover below 15% was selected because the median percent cover for giant salvinia cover across all three site types from September through February was 15%. If plant cover of $\leq 15\%$ was measured during this period, then the site was considered "controlled." In our study area, giant salvinia is never eradicated (0% cover). Thus, we chose the median percent cover value from September through February because this is when giant salvinia cover is generally the lowest. Additionally, when we tried other values for giant salvinia cover (e.g., 0, 5, and 10%), models would not converge because cover at most sites never fell below 15%. Because of logistics in the data collection process, the number of samples among all variables was not the same at each sampling location. Thus, instead of "dropping" data, we filled in missing data (e.g., giant salvinia cover, SAV cover, or weevil densities) for a sampling location using the variable's median for that specific sampling location that month (Dong and Peng 2013). For example, if only three giant salvinia samples were collected to assess weevil densities, but there were five giant salvinia cover estimates recorded, the median of those three weevil densities was used to fill in the missing two. Multiple subsamples at each sampling location in June were aggregated into a single observation using the mean for all measurements. Nested *k*-fold cross-validation (Cawley and Talbot 2010) with 10 folds in both the outer and inner loop was used to select the best model by minimizing mean absolute error. When performing nested cross-validation, contrary to nonnested *k*-fold cross-validation, there is typically no single best model; rather, there are a host of (typically similar) best models. This is because of the nature of nested cross-validation, which incorporates multiple different test sets to evaluate performance. In this instance the GLM Poisson regression with 15 and 10 folds was used.

Predicting dissolved oxygen levels. A multivariate adaptive regression splines (MARS) model was developed to estimate dissolved oxygen levels at any time of the season based on the time of year (month), giant salvinia cover, SAV cover, water temperature, and site type. A generalized linear model (GLM) was also developed to predict the time until dissolved oxygen levels reach above 5 mg L^{-1} or above based on giant salvinia percent cover, SAV percent cover, water temperature, and site type. Both models are important because, using these four variables, land managers can estimate current and future dissolved oxygen levels without purchasing costly instruments. Also, estimating current and future dissolved oxygen levels could help land managers make short- and long-term control decisions for their infestations. We selected 5 mg L^{-1} as the threshold to signify recovery since it represents the level at which fish become stressed (Chapman and Kimstach 1996; Flores and Carlson 2006).

We used MARS (Milborrow 2023; R Core Team 2020) to estimate dissolved oxygen levels at any time of the season based on the values for giant salvinia cover, SAV cover, water temperature, and site type. The MARS technique is a is a nonparametric, flexible, and data-driven regression technique that seeks to model the relationship between a response variable and one or more predictor variables. It is particularly useful for high-dimensional data, complex interactions, and nonlinear relationships, and works by building a piecewise linear regression model, which consists of basis functions (splines). These splines are generated by recursively partitioning the predictor space using binary splits (knots) and fitting linear models to each partition. The final model is obtained by selecting the best combination of basis functions through a two-step process: forward selection and backward elimination. Forward selection involves iteratively adding basis functions to the model to minimize the residual sum of squares. Backward elimination then prunes the model, removing basis functions that contribute the least to the model's performance, based on a penalty for model complexity. This helps prevent overfitting and results in a more parsimonious model.

The technique is an expansion on linear regression (e.g., ordinary least squares, GLM with Poisson link) to account for nonlinearity in the relationship between the input and output. The MARS model can also pick up on interactions automatically and detect nonlinearities in the relationships between independent and dependent variables. Thus, the MARS allows the model to select what interactions among the independent variables are significant when estimating dissolved oxygen levels at any time of the season. The MARS technique has been recently used to model changes in dissolved oxygen (Heddam and Kisi 2018; Nacar et al. 2020), eutrophication (Fernández et al. 2014), and species distribution (Leathwick et al. 2004) in natural habitats.

Two important hyperparameters associated with a MARS model are the maximum degree of interactions and the number of terms retained in the final model. The MARS model was selected because it had a lower average root mean square error than linear regression during each iteration of nested *k*-fold cross-validation (Supplemental Table 1). We compared different "versions" of the MARS model with different hyperparameter choices, namely, the degree of interaction from 1, 2, 3, 4 (four choices) and the number of terms retained from 1, 3, 7, 10, 13, 15, 18, 20, and 25 (nine choices). Thus, there were 36 (4×9) different "versions" of the MARS model. The "best" MARS model was selected based on the lowest average cross-validation error using grid search. In our case the "best" order of interaction was two, and the "best" number of terms retained was 15.

A generalized linear model (GLM), with a log link and Poisson distribution, was also developed to estimate the time (number of months) it takes from June until dissolved oxygen levels reach above 5 mg L^{-1}. The independent variables selected for the model were giant salvinia percent cover, SAV percent cover, water temperature, and site type in June. We created the dependent variable "time in months" to estimate how many months it takes, beginning in June until dissolved oxygen levels were above 5 mg L^{-1} using the following formula:

$$\begin{aligned}\text{Log(time in months)} = \text{intercept} & \\ + [(\beta_0 \times \text{giant salvinia cover}) & \\ +(\beta_1 \times \text{SAV cover}) & \\ +(\beta_2 \times \text{water temperature}) & \\ +(\beta_3 \times \text{site type})]. &\end{aligned}$$

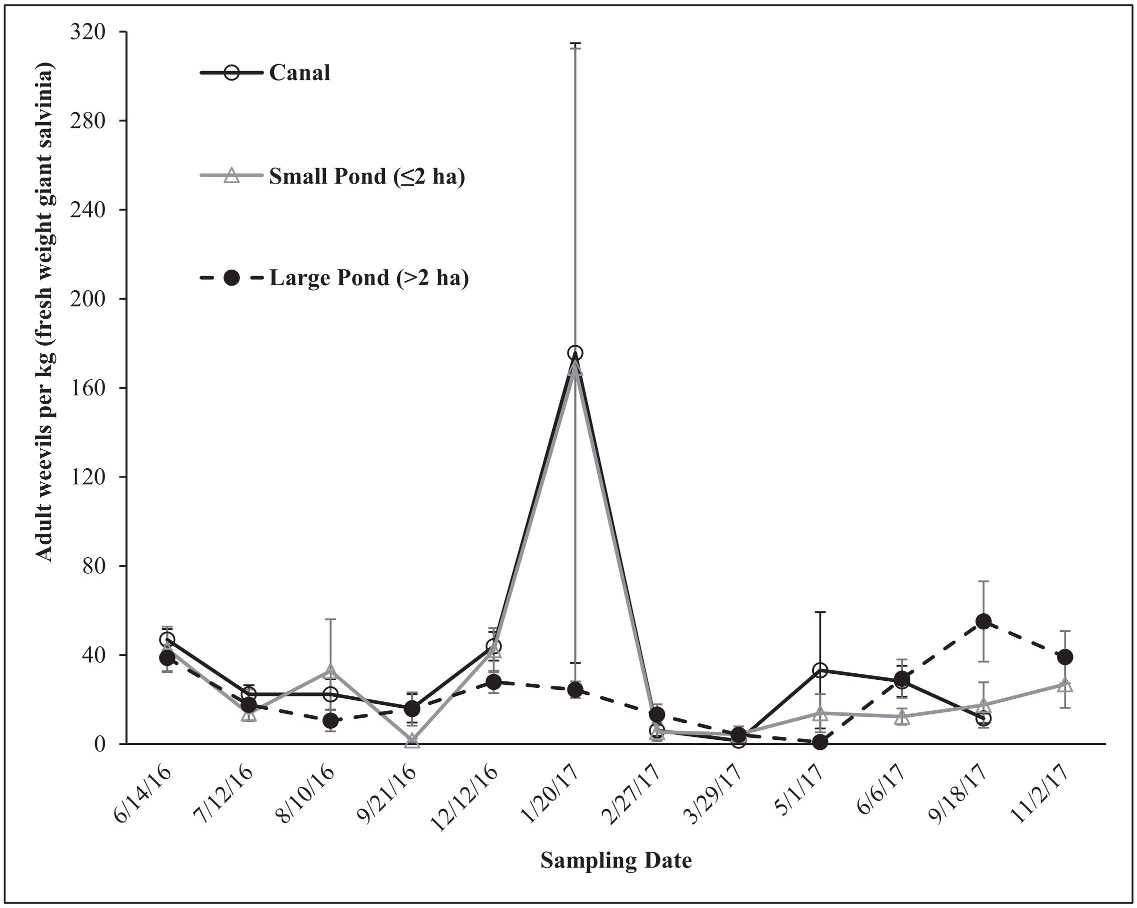

Figure 2. Comparison of mean adult weevil densities (± S.E.) at each site type (canal, small pond, and large pond) from June 2016 to November 2017. Trends in mean adult weevil densities were similar between the three site types during the study; however, in January 2017, adult weevil densities were higher in small ponds and canals relative to large ponds. Though mean adult weevil densities appeared higher in small ponds and canals in January 2017, the high standard errors for these site types suggest that densities varied considerably.

Nested cross-validation was used where a Poisson regression had a lower root mean square error than the MARS model, and thus was a better model for predicting the time until dissolved oxygen levels reached 5 mg L^{-1} or above. Fifteen-fold cross-validation was performed in the outer loop with 10-fold cross-validation performed in the inner loop. Again, the GLM Poisson regression with 15 and 10 folds was used. In both models, missing cover and weevil data for a sampling location were filled using the median for that specific sampling location that month as described above (Dong and Peng 2013). Next, multiple subsamples at each sampling location in June were aggregated into a single observation using the mean for all measurements. The criterion for determining if a site reached above 5 mg L^{-1} was if a measurement was above 5 mg L^{-1}, then that satisfied the criteria.

RESULTS AND DISCUSSION

Adult salvinia weevil phenology

Despite the lack of field releases for two years, salvinia weevils were able to maintain populations to control giant salvinia infestations in the study area, and densities were similar between the three site types (Figure 2). Population levels of salvinia weevils in June 2016 were likely due to reproductive activity during the spring (March and April) and to the lack of cold winter or spring temperatures (Mukherjee et al. 2014; Nachtrieb et al. 2020; Wahl and Diaz 2020). During the spring of 2016, spring temperatures were mild, which likely promoted the survival of overwintering adults (Mukherjee et al. 2014; Wahl and Diaz 2020). In addition, there were no disturbances associated with floods, saltwater intrusion, or hurricanes, which are major disturbances in coastal Louisiana. However, enhanced storm activity in the Gulf of Mexico (Dietz et al. 2018) may negatively impact the overwinter generation of adult weevils more frequently in the future. While not statistically analyzed, adult weevil densities (mean ± S.E.) in January 2017 appeared greater in small ponds (169.1 ± 143.3 kg^{-1}) and canals (175.6 ± 139.2 kg^{-1}) relative to large ponds (24.4 ± 3.7 kg^{-1}) (Figure 2); however, the high error associated with the mean values suggest no statistical difference. Weevil densities during this time could be an artifact of the low coverage of giant salvinia, suggesting aggregations of weevils in any food available.

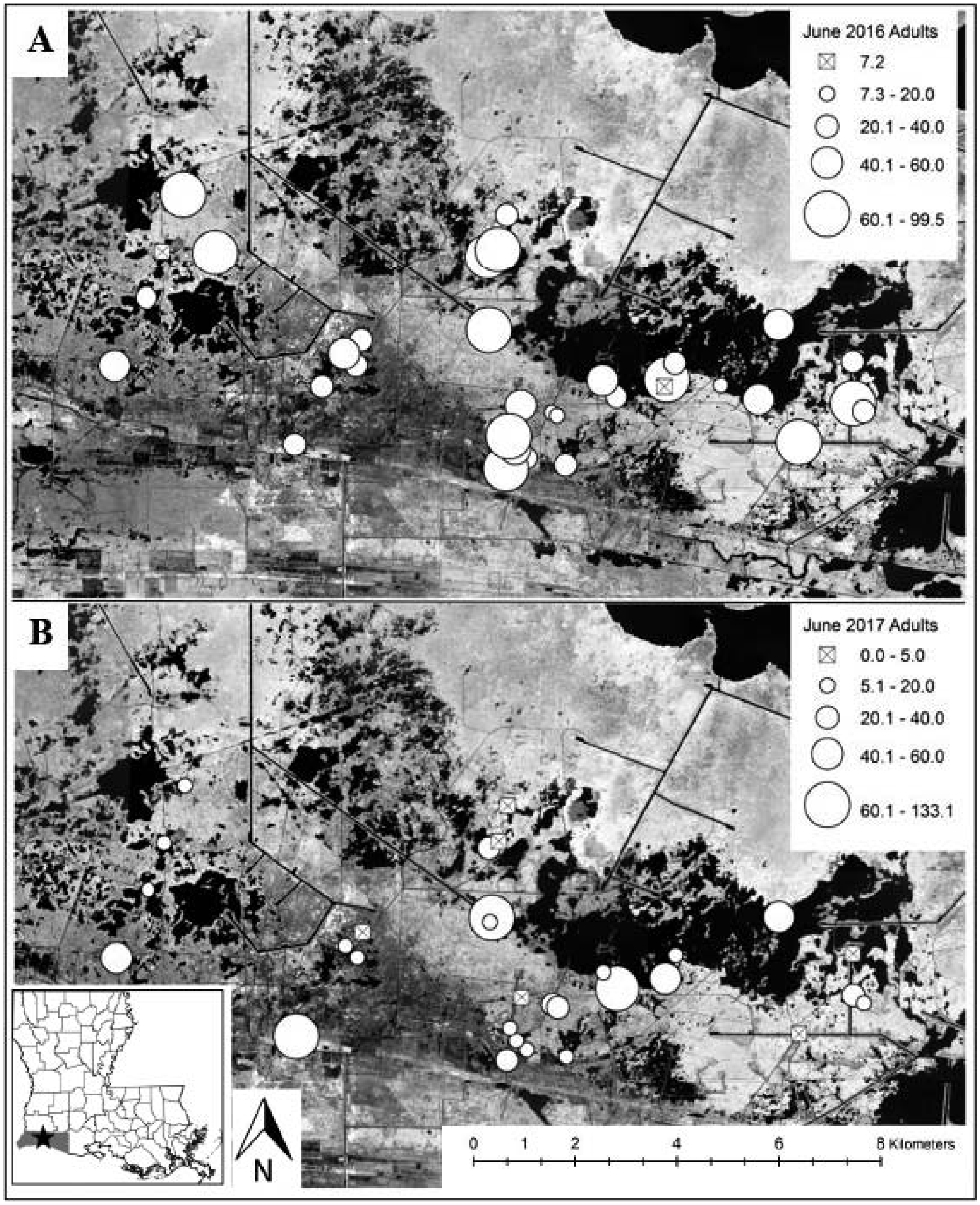

Figure 3. Distribution of weevil densities in Cameron Parish in southwestern Louisiana during June: (A) 2016 and (B) 2017. The larger the circle the higher the adult weevil densities were in that area. In both years adult weevil densities varied across the wetland landscape.

Distribution of adult salvinia weevils in June

In both years, adult weevils were present at most sampling locations and found in each site type (Figures 3A and 3B). In June 2016, mean adult weevil densities were 46.9 kg^{-1} (range, 5.6 to 113.4 kg^{-1}) in canals, 42.5 kg^{-1} (range, 0 to 119.2 kg^{-1}) in small ponds, and 38.7 kg^{-1} (range, 2.8 to 104.8 kg^{-1}) in large ponds (Supplemental Table 2). In June 2017 mean adult weevil densities were 28.2 kg^{-1} (range, 0 to 154.8 kg^{-1}) in canals, 12.3 kg^{-1} (range, 0 to 26.9 kg^{-1}) in small ponds, and 29.4 kg^{-1} (range, 0 to 113.2 kg^{-1}) in large ponds (Supplemental Table 2).

Our data display that adult weevils were distributed across the wetland landscape and were present throughout both sampling years (Figure 3). Densities might be explained by an uneven dispersal of individuals due to environmental conditions (e.g., wind and hydrologic flow) resulting in high-density variation across the landscape (Grodowitz et al. 2014). This is driven in part by the patchiness of the southwest Louisiana wetlands. Ponds connected to canals

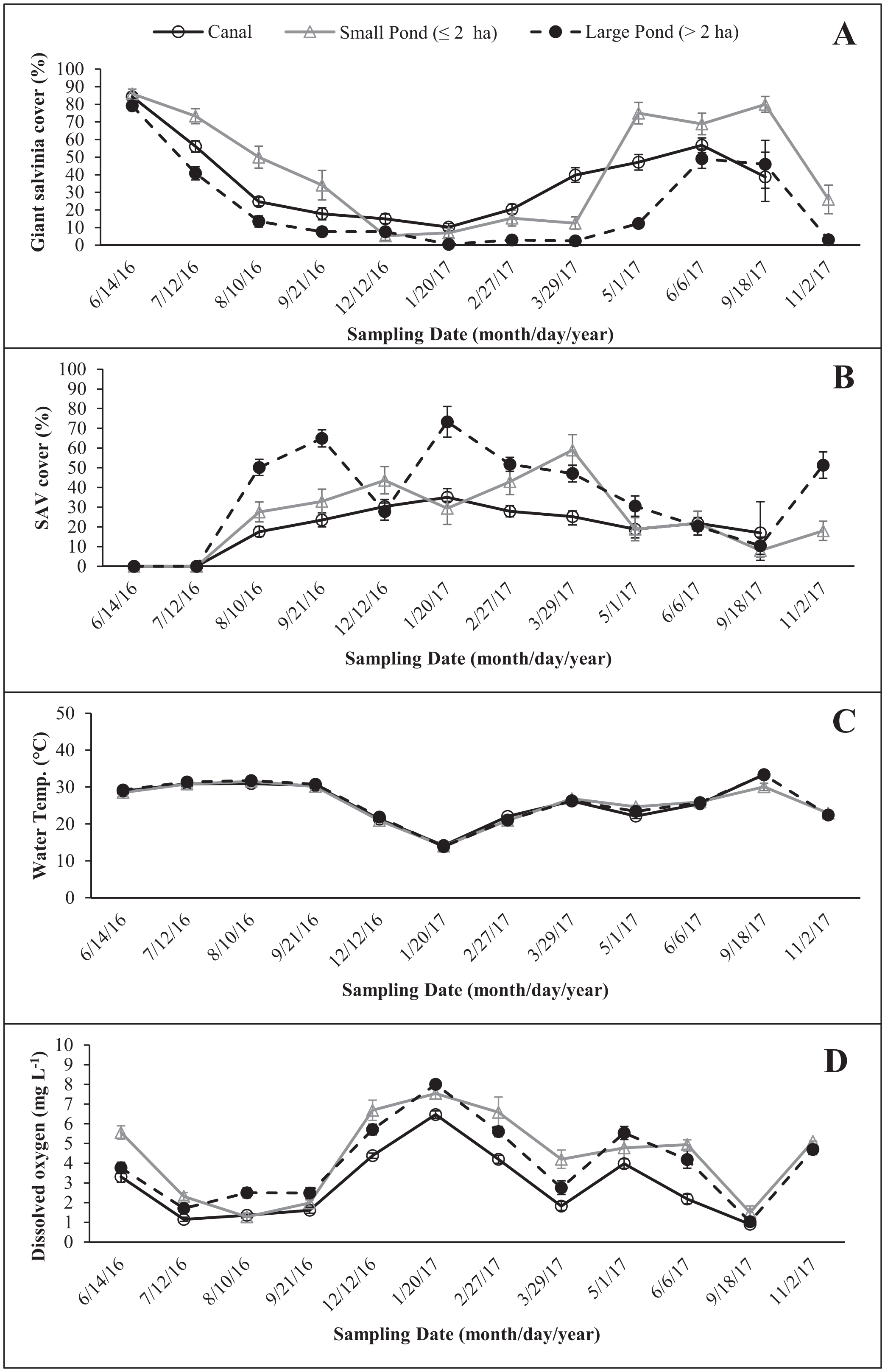

Figure 4. Comparison of mean (± S.E.) (A) giant salvinia cover, (B) submersed aquatic vegetation (SAV) cover, (C) water temperature, and (D) dissolved oxygen between the three site types (canal, small pond, and large pond) from June 2016 to early November 2017. As giant salvinia cover decreased (A), SAV cover (B) and dissolved oxygen levels (C) increased. This illustrates that as giant salvinia covers the surface of a waterbody, SAV cover decreases from lack of sunlight. Consequently, dissolved oxygen levels decrease from the lack of oxygen being produced by SAV.

would have a greater chance of salvinia weevil colonization due to the connectivity to the rest of the landscape, but this also makes these ponds high risk for reinvasion of giant salvinia following control. Because canals connect the landscape in southwestern Louisiana, infestations in these waterways are important to monitor. The patchiness of salvinia weevil densities (Grodowitz et al. 2014) may also be explained by the limited flying ability of adults (Micinski et al. 2016). When giant salvinia is matted, weevils can easily disperse to higher-quality plants by walking, resulting in a localized increase in densities. The formation of a salvinia mat following winter may take longer in large ponds, relative to canals and small ponds, because of the large water surface area, therefore limiting the dispersal of weevils to large ponds until a large proportion of the surface is covered. Natural colonization of salvinia weevils in large ponds may take more time (e.g., months) because these locations are more isolated and delayed salvinia mat formation, limiting weevil establishment and population structure (e.g., abundance and dispersal). Managers should increase salvinia weevil densities in all three site types by moving infested plants from adjacent sites or a mass-rearing facility (Wahl and Diaz 2020).

Trends in giant salvinia cover, SAV cover, water temperature, and dissolved oxygen levels

Giant salvinia cover declined at all three site types from June 2016 to January 2017 (Figure 4A). From June 2016 to January 2017, giant salvinia cover decreased by 79% in small ponds, 74.3% in canals, and 78.7% in large ponds. From January to May 2017, giant salvinia cover increased in all three site types (Figure 4A). During this period, giant salvinia increased by 36.8, 68.0, and 12.0%, in the canal, small pond, and large pond site types, respectively. From May to September 2017, giant salvinia cover increased by 18.9% in the small pond site type but declined by 18.0 and 3.2% in canals and large ponds, respectively. Giant salvinia declined by 60.0% in the small pond and 42.8% in the large pond site types from September to November 2017 (Figure 4A). The GLMM found differences existed in giant salvinia cover among site types ($\chi^2 = 146$, df = 2, $P < 0.0001$), date ($\chi^2 = 9{,}474$, df = 11. $P < 0.0001$), and the interactions of site type with date ($\chi^2 = 4{,}335$, df = 21, $P < 0.0001$; Supplemental Table 3).

As giant salvinia cover declined, SAV cover increased (Figures 4A and 4B). In July 2016, SAV was absent (0%) at all three site types but increased by 29.4, 35, and 73.3% in small ponds, canals, and large ponds, respectively, from July 2016 to January 2017 (Figure 4B). From January to September 2017, SAV cover steadily declined by 21.4, 18, and 62.7% in the small pond, canal, and large pond site types, respectively (Figure 4B). From September to November 2017, SAV cover increased by 10% in small ponds and 41.3% in large ponds (Figure 4B). The GLMM found differences existed in SAV cover among site types ($\chi^2 = 17$, df = 2, $P = 0.0001$), date ($\chi^2 = 161$, df = 11, $P < 0.0001$), and the interaction of site type with date ($\chi^2 = 203$, df = 21, $P < 0.0001$; Supplemental Table 4).

Water temperature declined from June 2016 to January 2017 by more than 14 C at all three site types (Figure 4C). From January to September 2017, water temperature increased 16.1 C in small ponds and 19.5 and 19.2 C in large ponds and canals, respectively (Figure 4C). From September to November 2017, water temperature decreased by 11 C in large ponds and 7.2 C in small ponds (Figure 4C). Water temperature variation was explained by date ($\chi^2 = 1{,}704$, df = 11, $P < 0.0001$) but did not differ among site types or the interaction with site type with date.

Following the increase in SAV cover, dissolved oxygen levels increased (Figures 4B and 4D). From June to July 2016, dissolved oxygen levels fell by 3.2, 2.2, and 2.1 mg L^{-1} in the small pond, canal, and large pond site types, respectively (Figure 4C). Dissolved oxygen increased in all three site types from September 2016 (small pond: 2; canal: 0.9; large pond: 2.5 mg L^{-1}) to January 2017 (small pond: 7.5; canal: 6.5; large pond: 8 mg L^{-1}) (Figure 4C). The same trend in dissolved oxygen levels occurred from September 2017 to November 2017 in the small pond and large pond site types (Figure 4C). The LMM found differences in dissolved oxygen existed among site types ($\chi^2 = 9.42$, df = 2, $P < 0.01$), date ($\chi^2 = 821$, df = 11, $P < 0.0001$), and the interaction of site type with date ($\chi^2 = 100$, df = 21, $P < 0.0001$; Supplemental Table 5).

Submerged aquatic vegetation recovered quickly following the reduction of giant salvinia (Figure 4A and 4B). The recovery of SAV results in increased food and habitat for fish, waterfowl, and invertebrates (Poirrier et al. 2010; Van Driesche et al. 2010; Wahl et al. 2021a). Following biocontrol of giant salvinia, Motitsoe et al. (2020b) showed that aquatic communities recovered quickly and subsequently increased food chain length and biodiversity. Cultural and recreation activities, such as hunting, fishing, and wildlife observation, would return after giant salvinia removal and SAV rebounds. With early season monitoring, land managers can make more informed decisions as to whether they need to add more weevils to their infestation to control giant salvinia quickly and restore the SAV community.

Predicting giant salvinia control

The small pond site type was the only independent variable that had a significant effect on the time it takes to reduce giant salvinia cover to 15% (Table 1); however, we were not concerned with the individual or interaction effects of each variable but rather the linear relationship among the variables. In addition, MARS does detect interactions; however, since it performed worse than GLM, this means any interactions detected were not meaningful in creating the "best" model for prediction; thus, the GLM with the additive structure was "best."

Using the coefficients from Table 1, the following equation was developed to predict the amount of time it takes to reduce giant salvinia cover to 15%:

$$\begin{aligned}\text{Log(time in months)} = -0.243 &\\ + [(-0.003 \times \text{adult weevil density}) &\\ +(0.016 \times \text{giant salvinia cover}) &\\ +(\beta \times \text{site type})].&\end{aligned}$$

For the site-type coefficient (β), the canal site type was the reference group; thus, one would use 0 if their site type

Table 1. Generalized linear model (GLM) summary for predicting the time it takes until giant salvinia cover is below 15%. The small pond site type was the only independent variable that had a significant effect on the time it takes to reduce giant salvinia cover to 15%.

Variable	Coefficient	S.E.	*Z* value	*P* value
Intercept	−0.243	1.061	−0.229	0.8187
Adult weevils	−0.003	0.007	−0.489	0.6184
Giant salvinia cover	0.016	0.011	1.440	0.1499
Small pond (≤ 2 ha)	0.672	0.271	2.482	0.0131*
Large pond (> 2 ha)	−0.037	0.353	−0.104	0.9170

An asterisk (*) indicates significance ($\alpha < 0.050$).

were a canal, 0.672 if their site type were a small pond, or –0.037 if their site type was a large pond. The coefficient for adult weevil density, –0.003, means that holding giant salvinia cover and site type constant, increasing adults by 1 adult per kg in June equates to a 0.3% reduction in the mean number of months until giant salvinia cover is below 15%. The coefficient for giant salvinia cover, 0.016, means that holding adult weevils and site type constant, increasing giant salvinia cover by 1% in June equates to a 1.6% increase in the mean number of months until giant salvinia cover is below 15%. Holding adult weevils and giant salvinia cover constant going from a canal to a small pond equates to a 95% increase ($e^{0.672} = 1.95$ times longer = 95% longer) in the mean months until giant salvinia is below 15%. Stated differently, it takes roughly twice as long for the weevils to reduce giant salvinia cover in a small pond versus a canal. Holding adults and giant salvinia cover constant going from a canal to a large pond equates to a 2.95% reduction ($e^{-0.037} = 0.97$ times longer = 2.95% longer) in the mean months until giant salvinia cover is below 15%.

Conditions leading to the rapid population growth of salvinia weevils include giant salvinia quality since adults prefer buds that are nitrogen-rich (Room and Thomas 1986; Julien et al. 1987; Nachtrieb 2014). Weevils were beginning to control salvinia in June 2016 and caused salvinia cover to decrease and SAV to increase as the year progressed. As winter approached, herbivore pressure was relaxed due to the thermal restraints of the weevil. This allowed salvinia, in part, to persist through winter and then rapidly grow during spring. The increase in temperature, coupled with the production of new buds with high nitrogen content, stimulates the reproduction and population growth of weevils, leading to increased densities in late spring through fall. Estimating the length of time for biological control has been a question that has eluded resource managers. The natural variation in salvinia weevil densities means some infestations will be controlled faster than others (Grodowitz et al. 2014). By knowing plant cover, weevil density, and habitat type (canal, small, large pond) managers can apply this equation to estimate months until control. Table 2 shows the different lengths of time it takes until giant salvinia cover is below 15% in a small pond based on different salvinia weevil densities and giant salvinia coverage in June. Based on site conditions land managers can improve their decisions, such as the reintroduction of salvinia weevils or the application of other forms of control, to decrease the control time.

Table 2. This matrix shows time (months) estimates to reduce giant salvinia cover below 15% based on giant salvinia cover and adult weevil densities in June in a small pond (≤ 2 ha) location. The time estimates are in months, and the number in parentheses is the time in days. We converted months to days by taking the time in months and multiplying it by 30, the average amount of days in a month. As the initial giant salvinia cover (%) increases at a site is higher, the time it takes to reduce its cover below 15% takes longer. Similarly, if the initial adult weevil density is low, it will take longer to suppress giant salvinia cover below 15% versus if you have a higher initial population of adults.

Giant salvinia cover (%)	Adult weevil density (per kg of giant salvinia fresh weight)			
	5	10	20	40
5	2.26 (68)	2.22 (67)	2.16 (65)	2.03 (61)
50	3.37 (101)	3.32 (100)	3.22 (97)	3.03 (91)
75	5.02 (151)	4.95 (148)	4.8 (144)	4.52 (136)
100	7.49 (225)	7.38 (221)	7.16 (215)	6.75 (202)

Predicting dissolved oxygen level

Multivariate adaptive regression splines (MARS). The multivariate adaptive regression splines (MARS) coefficients for the independent variables and interaction among the variables for estimating dissolved oxygen levels at any given time during the season are shown in Table 3. Coefficients represent a directional effect on predicted dissolved oxygen level (e.g., positive or negative). However, the larger the coefficient does not mean it is a "more important" variable

Table 3. Multivariate adaptive regression splines (MARS) coefficients summary for estimating dissolved oxygen levels at any given time of the season based on the values of the independent variables: time of year (month), giant salvinia cover, SAV cover, water temperature, and site type. Coefficients represent a directional effect on predicted dissolved oxygen level, but a larger coefficient does not mean it is "more important" since the independent variables are all on different scales. Each hinge can be interpreted as an "if-else" statement. For example, if giant salvinia cover is less than 60%, then use the coefficient –0.01, else use –0.04 if giant salvinia cover is greater than 60%. The small pond is the only site type shown because the canal and large pond site types were negligible in terms of their effect on dissolved oxygen levels.

Model output (variable or interaction: hinge)[1]	Coefficient
Intercept	6.36
Small pond (≤ 2 ha)	1.01
Giant salvinia cover (%): *h*(60-giant salvinia cover)	−0.01
Giant salvinia cover (%): *h*(giant salvinia cover-60)	−0.04
SAV cover (%): *h*(SAV cover-50)	0.03
Water temperature (C): *h*(water temperature-13.5)	−0.20
Months since June: *h*(7-months since June)	−1.05
Months before June: *h*(months since June-7)	−1.03
Giant salvinia cover (%) × water temperature (C): *h*(60-giant salvinia cover) × *h*(water temperature-31.6)	0.02
Giant salvinia cover (%) × months since June: *h*(60-giant salvinia cover) × *h*(months since June-1)	0.01
Giant salvinia cover (%) × months since June: *h*(60-giant salvinia cover) × *h*(1-months since June)	0.05
SAV cover (%) × water temperature (C): *h*(50-SAV cover) × *h*(water temperature-28.99)	−0.01
SAV cover (%) × months since June: *h*(50-SAV cover) × *h*(2-months since June)	0.04
Water temperature (C) × months since June: *h*(water temperature-13.5) × *h*(months since June-9)	0.18
Water temperature (C) × months since June: *h*(water temperature-13.5) × *h*(9-months since June)	0.03

[1] $h(x\text{-}a)$ is a hinge function with a cut point a along a variable x.

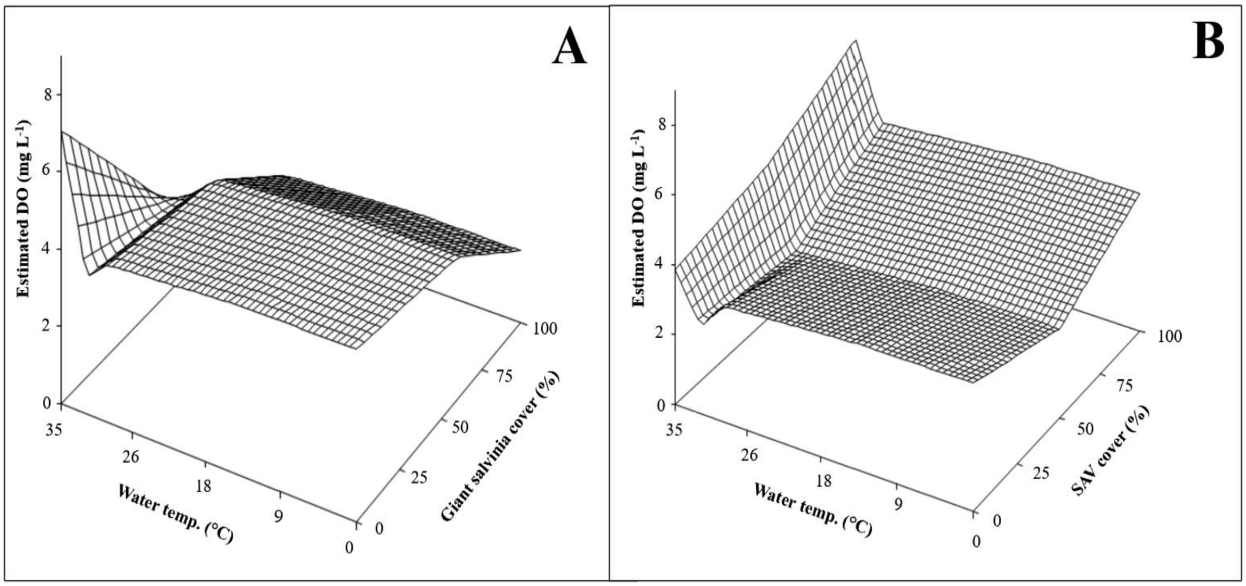

Figure 5. 3D plots showing the dynamics between giant salvinia cover (%), submerged aquatic vegetation cover (%), and water temperature (C) on dissolved oxygen (mg L^{-1}). Dissolved oxygen values range from less than 2 to above 6 mg L^{-1}. (A) The interaction effects between giant salvinia cover and water temperature on dissolved oxygen. Dissolved oxygen levels decrease as giant salvinia cover increases, and dissolved oxygen levels are lowest when giant salvinia cover is high and water temperatures are warm. (B) The interaction effects between submerged aquatic vegetation and water temperature on dissolved oxygen. As the percent cover of SAVs increases, dissolved oxygen levels increase even as water temperatures warm. Interestingly the slight dip, creating a "V shape," shows that dissolved oxygen levels fall while submerged aquatic vegetation is increasing.

since the input variables are all on different scales (e.g., temperature, months since June, giant salvinia cover, etc.). The model output and associated hinge can be interpreted as an "if-else" statement. For example, if giant salvinia cover is less than 60%, then use the coefficient –0.01, else use –0.04 if giant salvinia cover is greater than 60% (Table 3). Coefficients are used in front of the "if-else" statement, thus if giant salvinia cover is 50%, then that hinge would be –0.01(60 to 50) = –0.1. This means that if giant salvinia cover is 50%, then there would be a –0.1 decrease in the predicted dissolved oxygen level. The small pond is the only site type shown because the canal and large pond site types were negligible in terms of their effect on dissolved oxygen levels. The small pond coefficient of 1.01 means that being a small pond leads to a 1.01 increase in the predicted dissolved oxygen level.

An example of how the MARS model would be applied in two different situations to estimate dissolved oxygen levels in September is shown in Supplemental Table 6. In the two situations, water temperature (20 C), site type (small pond), and month (09) are the same; however, giant salvinia and SAV cover differ by 55% and 70%, respectively. In this example, using the associated coefficients for each hinge function (if-else statement) a small pond in September with less giant salvinia and greater SAV cover had 1.9 mg L^{-1} more dissolved oxygen.

The MARS model predicted that dissolved oxygen levels decrease as giant salvinia cover increases, and dissolved oxygen levels are lowest when giant salvinia cover is high and water temperatures are warm (Figure 5A). Oppositely, dissolved oxygen levels are highest when giant salvinia cover is low even when water temperatures are higher (Figure 5A). As the percent cover of SAVs increases, dissolved oxygen levels increase even as water temperatures warm. Interestingly the slight dip, creating a "V shape" shows that dissolved oxygen levels fall while submerged aquatic vegetation is increasing (Figure 5B). Overall, Figure 5 demonstrates how much giant salvinia and SAV cover affect dissolved oxygen levels.

Generalized linear model (GLM). Giant salvinia cover, SAV cover, and water temperature, along with site type (canal, small pond, and large pond), had no significant effect on the time (months) until dissolved oxygen levels were above 5 mg L^{-1} (Table 4). However, we were not concerned about the individual or interaction effects of the variables. Instead, we were interested in the linear relationship among the variables for estimating the time until dissolved oxygen levels reach 5 mg L^{-1}.

Using the coefficients in Table 4, the following equation was developed:

$$\begin{aligned}\text{Log(time in months)} = {} & -2.794 \\ & + [(0.003 \times \text{giant salvinia cover}) \\ & \quad + (-0.004 \times \text{SAV cover}) \\ & \quad + (0.167 \times \text{water temperature}) \\ & \quad + (\beta_3 \times \text{site type})].\end{aligned}$$

For the site type coefficient (β), the canal site type was the reference group; thus, one would use 0 if their site type were a canal, –0.247 if their site type were a small pond, or –0.332 if their site type was a large pond. The coefficient for giant salvinia cover, 0.003, meant that holding the other independent variables constant, increasing giant salvinia cover by 1% in June would equate to a 0.3% increase in the mean number of months until dissolved oxygen was above 5 mg L^{-1}.

The coefficient for SAV cover, –0.004, means that holding the other independent variables constant, increas-

TABLE 4. GENERALIZED LINEAR MODEL (GLM) COEFFICIENTS SUMMARY FOR PREDICTING THE TIME IT TAKES UNTIL DISSOLVED OXYGEN LEVELS ARE ABOVE 5 MG L^{-1}. GIANT SALVINIA COVER, SAV COVER, WATER TEMPERATURE, AND SITE TYPE (CANAL, SMALL POND, AND LARGE POND) HAD NO SIGNIFICANT EFFECT ON THE TIME (MONTHS) UNTIL DISSOLVED OXYGEN LEVELS WERE ABOVE 5 MG L^{-1}. HOWEVER, WE WERE INTERESTED IN THE LINEAR RELATIONSHIP AMONG THE VARIABLES FOR ESTIMATING THE TIME UNTIL DISSOLVED OXYGEN LEVELS REACH 5 MG L^{-1} AND NOT THE INDIVIDUAL EFFECTS OF EACH VARIABLE.

Variable	Coefficient	S.E.	*Z* value	*P* value
Intercept	−2.794	5.657	−0.494	0.621
Giant salvinia cover	0.003	0.008	0.372	0.710
SAV cover	−0.004	0.011	−0.341	0.733
Water temperature	0.167	0.194	0.862	0.389
Small pond ($\leq$ 2 ha)	−0.247	0.474	2.482	0.602
Large pond ($>$ 2 ha)	−0.332	0.229	−1.445	0.148

An asterisk (*) indicates significance ($\alpha < 0.050$).

ing SAV cover by 1% in June equates to a 0.4% decrease in the mean number of months until dissolved oxygen was above 5 mg L^{-1}. The coefficient for water temperature, 0.167, means that holding the other independent variables constant, increasing water temperature by 1 C in June equates to an 18% increase in the mean number of months until dissolved oxygen was above 5 mg L^{-1}. Holding all other independent variables constant, going from a canal to a small pond equates to a 22% reduction ($e^{-0.247} = 0.78$ times shorter = 22% shorter) in the mean months until dissolved oxygen is above 5 mg L^{-1}. Holding all other independent variables constant, going from a canal to a large pond equates to a 39% reduction ($e^{-0.332} = 0.72$ times shorter = 38% shorter) in the mean months until dissolved oxygen levels are above 5 mg L^{-1}.

Dissolved oxygen is a critical indicator of wetland health (U.S. EPA 2021) and a key indicator of the presence of SAV. Estimating dissolved oxygen levels is essential for knowing the habitat quality for fish and wildlife (e.g., adequate SAV cover and invertebrates for food). Applying our MARS model, land managers can assess baseline dissolved oxygen levels and track the seasonal dynamics between giant salvinia cover, SAV cover, water temperature, and dissolved oxygen. This tracking capability allows land managers to quantify seasonal changes in wetland dynamics. In addition to the MARS model, estimating the time to recover dissolved oxygen levels above the 5 mg L^{-1} threshold for fish (Chapman and Kimstach 1996; Flores and Carlson 2006) is vital for making more informed decisions regarding giant salvinia control. For example, considering a land management objective is to have open water and SAVs by September for waterfowl hunting, in June, the model predicts that dissolved oxygen will recover to levels above 5 mg L^{-1} by November. In that case, the land manager can release more weevils in early summer or select another control method to integrate. The capability of estimating the time to recover dissolved oxygen allows land managers to have more confidence in their decisions concerning giant salvinia control. Our results demonstrate the importance of monitoring salvinia weevil densities early in the season for estimating the timing of giant salvinia control and recovery of dissolved oxygen levels. Estimating the amount of time until recovery of ecosystem structure and function following invasive species disturbance is important for management decisions. However, numerous compounding variables make estimating this timeframe difficult. While not comprehensive, these models offer new insight to determine the duration of invasion through sampling only a few environmental variables. Once time until control is determined, managers could decrease recovery time by manipulating weevil densities in salvinia-impacted locations by releasing more weevils or deciding to implement another form of control. A land management agency may also develop a matrix using different percentages for giant salvinia cover and weevil densities to use in the field when estimating how long it will take the weevils to reduce giant salvinia. Our model could also provide a framework for developing similar models for invasive free-floating macrophytes, such as common water hyacinth (*Pontederia crassipes*), water lettuce (*Pistia stratiotes)*, duckweed (*Lemna* spp.), and their biocontrol agents. It is important to note that these models are specific to coastal semitropical wetlands conditions, and areas with different climates and wetland dynamics should apply these models cautiously.

SOURCES OF MATERIALS

[1] YSI ProDSS, YSI Incorporated, 1700 Brannum Ln., Yellow Springs, OH 45387.

[2] Frabill 3049 Wood Baitwell Net, Frabill Incorporated, 21121 Northwest Passage, Jackson, WI 53037.

[3] Ohaus SP2001 Scout Pro 2000 g Capacity × 0.1 g, Ohaus Corporation, 7 Campus Drive, Suite 310 Parsippany, NJ 07054.

[4] Nasco Whirl-Pak 4 oz, Whirl-Pak, Madison, WI 53716.

[5] ESRI Inc., 380 New York St., Redland, CA 92373, USA.

ACKNOWLEDGEMENTS

We would like to thank Louisiana State University Agriculture Center employees Fatima Nguyen, Emily Passman, Rachel Watson, Seth Spinner, Alana Russell, Lori Moshman, and Yi Wang for laboratory and field assistance. Miami Corporation graciously provided logistical support to conduct the surveys. We thank the Louisiana Department of Wildlife and Fisheries and the Coastal Protection and Restoration Authority for funding this project. This work was funded in part by the Louisiana State University Department of Entomology and the National Institute of Food and Agriculture, Hatch project accession number 1013004.

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