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RESEARCH

Management of Invasive Water Hyacinth as Both a Nuisance Weed and Invertebrate Habitat

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ABSTRACT

Invasive species have many detrimental ecological and socio-economic effects. However, invasive species can also provide novel habitat for native species. The growing rate of biological invasions world-wide presents an urgent dilemma: how can natural resource managers minimize negative effects of invasive species without depleting native taxa that have come to rely on them? Adaptive management can provide a means to address this dilemma when invasive species management plans are crafted in novel environments. We present a case study of research in support of adaptive management that considers the role of invasive water hyacinth (*Eichhornia crassipes* [Mart.] Solms [Pontederiaceae]) management, using herbicides, in aquatic food web functioning in the Sacramento–San Joaquin River Delta of California, USA (the "Delta"). We hypothesized that herbicide applications under current management protocols would reduce the abundance and diversity of aquatic invertebrates because they would alter both structural and biological habitat. Using a Before, After, Control, Intervention (BACI) experiment, we sampled invertebrates per gram plant biomass before and 4 weeks after glyphosate applications in treated and untreated locations. There was more plant biomass in the late-season samples because dead, dying, and living plant materials were compacted. However, there were no detectable differences between control and treated sites—or for samples before versus after the treatment date—for invertebrate abundance, species richness, or evenness. This case study demonstrates that even decaying water hyacinth serves as habitat for invertebrates that may be forage for Delta fishes. We concluded that current management practices using glyphosate do not affect invertebrate abundance during a month-long period of weed decay. These results provide valuable feedback for the "evaluate and respond" component of the adaptive management process for water hyacinth control, and demonstrate how managers globally can and should consider potential food web effects in the course of their invasive species management efforts.

KEY WORDS

Adaptive management, aquatic food web, invasive macrophyte, macroinvertebrate, non-target effects, novel ecosystem, Sacramento–San Joaquin River Delta, water hyacinth

INTRODUCTION

Invasive species have a multitude of ecological and socio-economic effects, and can play a strong role in ecosystem functioning (Williams et al. 1989; Vitousek et al. 1997; Mack et al. 2000; Pimentel et al. 2001; D'Antonio and Meyerson 2002, etc.). However, eradication of invasive species is expensive and difficult: globally, only ~50% of eradication attempts are successful, and success rates are substantially lower in semi-natural habitats relative to man-made environments such as greenhouses (Pluess et al. 2012). Additionally, invasive species can become community mainstays and assume novel ecological roles in the environments they invade (e.g., Hobbs et al. 2009; Holzer and Lawler 2015). In some cases, reducing invasive species can have strong habitat implications for native species of conservation concern. Therefore, if the invading species is eradicated without other restoration activities, native organisms may experience negative consequences (Davis et al. 2011). Scenarios like these are increasingly common around the world and present an urgent dilemma: how can natural resource managers minimize negative effects of invasive species without depleting native taxa that have come to rely on them? We address this question through our case study in the Sacramento–San Joaquin River Delta.

CASE STUDY: Water Hyacinth in the Sacramento–San Joaquin River Delta

In this case study, we examined whether water hyacinth (*Eichhornia crassipes*) management activities influence invertebrate communities that may support fishes of the Sacramento–San Joaquin River Delta (hereafter, the "Delta"). The Delta is part of the largest estuary on the Pacific Coast of the Americas, and serves as a critical link between California's water supply, aquatic species, and human populations. The Delta faces many challenges that have been described extensively by natural resources agencies and researchers (i.e., Lund et al. 2007; DSC 2016, etc.). Aquatic invasive species are of great concern in the Delta because they can affect ecological communities, water distribution, commerce, recreation, and other human industries (Cohen and Carlton 1998; Brown et al. 2007; Mount et al. 2012; Hanak et al. 2013). For these and other reasons, the Delta is an ecosystem with novel features—"abiotic, biotic, and social components (and their interactions) that, by virtue of human influence, differs from those that prevailed historically, having a tendency to self-organize and manifest novel qualities without intensive human management" (Hobbs et al. 2009). Water hyacinth is one of the most visible invaders in the Delta, because it is a floating aquatic weed and is found nearly Delta-wide.

Historically, much of the Delta, including our study location, was characterized by freshwater emergent wetlands (Whipple et al. 2012). Vegetated littoral zones like these are important for producing invertebrate biomass as food for threatened and endangered juvenile salmonids and other fishes that forage on insects and zooplankton (Fresh 2006; Hampton et al. 2011; Naiman et al. 2012; del Rosario et al. 2013; Goertler et al. 2015; Brown et al. 2016). However, only a small proportion of historic Delta freshwater wetlands remain today (Whipple et al. 2012). In the absence of the once-abundant Delta littoral native plant communities, invertebrates must use available habitats. Today, the littoral habitat includes water hyacinth throughout the Delta.

Invasive Water Hyacinth and Delta Aquatic Food Webs

Water hyacinth is a floating aquatic macrophyte native to the Amazon basin. It has invaded aquatic ecosystems around the world, affecting human endeavors as well as abiotic and biotic ecosystem elements. For example, Water hyacinth can block sunlight and alter turbidity levels; decrease phytoplankton production, dissolved oxygen (DO), and nutrient levels; and influence heavy metal concentrations (Villamagna et al. 2010). Water hyacinth can also clog navigable water ways, displace native vegetation, alter nutrient cycling, and change sediment dynamics (CDBW 2012; Khanna et al. 2012).

There is limited research that describes the role of water hyacinth in structuring and sustaining invertebrate communities. However, Villamagna et al. (2010) determined that, in general, water hyacinth increases habitat complexity but decreases food availability for invertebrates. Toft et al. (2003) demonstrated that—compared to a native macrophyte (*Hydrocotyle umbellata*)—water hyacinth had lower macroinvertebrate densities, and that the invertebrates found on water hyacinth were less prevalent in fish diets. Even so, water hyacinth has been a feature of the Delta for ~70 years, is widely dispersed, extremely abundant, and provides complex habitat for invertebrates. Given that water hyacinth is a major physical and biological feature of the Delta and serves as habitat for invertebrates that are common in the diets of some Delta fishes (Sommer et al. 2001; Gray et al. 2002; Moyle et al. 2004; Whitley and Bollens 2013; Howe et al. 2014), it is incumbent upon Delta managers to consider the implications of water hyacinth management on the species that use it as habitat.

Invasive Macrophyte Management in the Delta

In accordance with the Harbors and Navigation Code (2.1 HNC § 64), the California Parks Division of Boating and Waterways (CDBW) is the lead agency responsible for cooperating with state, local, and federal agencies in "identifying, detecting, controlling, and administering programs to manage invasive aquatic plants in the Sacramento–San Joaquin Delta, its tributaries, and the Suisun Marsh." In cooperation with the California Department of Fish and Wildlife, CDBW is tasked with evaluating the threat of aquatic invasive species to the environment, economy, and human health. Consequently, CDBW has undertaken programs to control water hyacinth, Brazilian waterweed (*Egeria densa*), and South American spongeplant (*Limnobium laevigatum*) in the Delta. The CDBW uses several techniques in its water hyacinth control program, including the use of herbicides (primarily glyphosate, 2,4-D and Agri-Dex) (CDBW 2012). Though it is imperative that water hyacinth in the Delta be managed—given its wide distribution, ability to block navigation, rapid growth rate, and sheer abundance—weed management activities in other ecosystems demonstrate that such actions may also alter habitat, hydrology, water quality, and food resources for aquatic invertebrates that are associated with invasive macrophytes (Monahan and Caffery 1996; Bicudo et al. 2007; Greenfield et al. 2007; Rzymski 2013). The CDBW prepares biological assessments of their management activities—including justification of the amount of herbicide applied—for regulatory review. In an effort to reduce the environmental effects of their operations over time, they also provide logistical support for on-going research (such as the study presented here) as part of their adaptive management process.

Widespread herbicide application in the Delta creates a mosaic of living and decaying water hyacinth that can persist for at least 4 weeks before the decaying material dissipates. Little is known about the macroinvertebrate communities within these decaying water hyacinth mats. It is difficult to predict how management will affect macroinvertebrates because decaying water hyacinth releases nutrients and organic particles that support the food web, but also feed bacterial communities that may drive DO down and subsequently negatively affect macroinvertabrates and zooplankton (Greenfield et al. 2007). We hypothesized that herbicide applications under current management protocols would reduce the abundance and diversity of aquatic invertebrates because they would alter structural and biological habitat.

Hypothesis Testing to Inform Adaptive Management

This study provides valuable information for the "evaluate and respond" component of the Delta Water Hyacinth Control Program (WHCP), which employs adaptive management: a systematic approach for improving resource management by learning from management outcomes (Holling 1978; Bormann 1999). This study also serves as a case study example for generating experimentally derived evidence to support adaptive management programs in other systems where water hyacinth is present (Bellamy et al. 2001; Nichols and Williams 2006). To ensure best practices in their management and policy operations, the CDBW has employed this work in their Section

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7 Biological Assessment with the United States Fish and Wildlife Service. This case study is also pertinent to management of novel ecosystems, where even non-native species can have important ecological roles (Schlaepfer et al. 2011). Since water hyacinth is intensively managed with herbicides on a global scale, this work has broad applicability and provides an example for future hypothesis-driven adaptive management efforts involving invasive plants' roles in ecosystem functioning.

METHODS

Study Location and Site Selection

Experimental sites were in the central Delta, California (USA), in water hyacinth mats that surround Bacon Island (Figure 1). We chose to focus our study on sites that surrounded Bacon Island because they had predictable herbicide treatment dates. Other site-selection criteria included: mats of floating water hyacinth that were likely to remain in place for the study's duration; mats at control sites that would remain untreated with herbicide; habitat characteristics similar enough to be comparable between and among treatment and control sites; and no other management activities by the CDBW.

Experimental Design

Using a Before, After, Control, Intervention (BACI) experimental design, we established five sampling sites to receive herbicide treatment with glyphosate, each paired with a control site that would not receive any herbicide treatment. CDBW applied glyphosate treatments (120 oz, AC) along with Agri-Dex (adjuvant) at treatment locations. Treatment dates varied among sites during spring and summer 2015 (see Appendix A, Table A1). During herbicide application, the CDBW left untreated buffer strips to comply with the agency's fish passage protocols that protect migrating and resident fish (CDBW 2012). However, for treated sites, we assumed that treatment effects would be detected throughout the site, across treated and untreated strips. To ensure this assumption matched reality, we randomly sampled across the entire spatial extent of mats at both treatment and control sites.

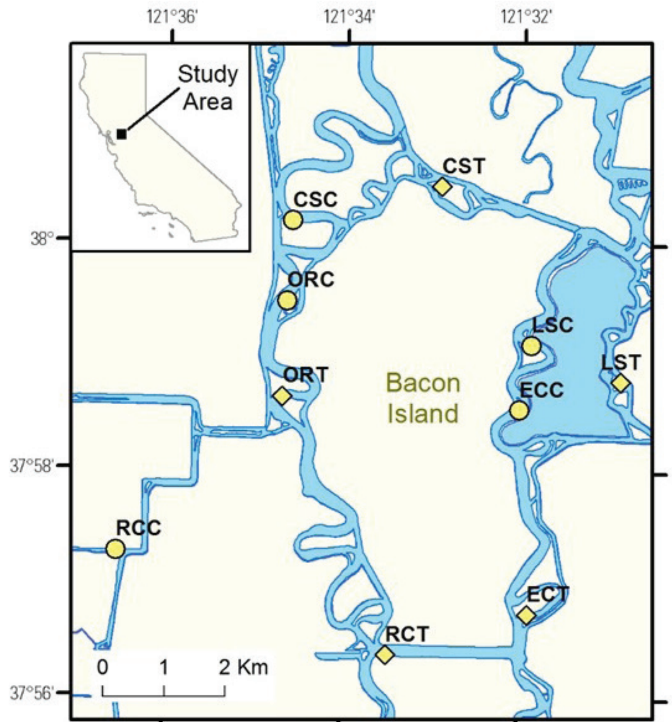

Figure 1 Map of experimental data collection sites in the central Delta. RCC=Railroad Cut Control, RCT = Railroad Cut Treatment, ECC = Empire Cut Control, ECT = Empire Cut Treatment, LSC = Latham Slough Control, LST = Latham Slough Treatment, CSC = Connection Slough Control, CST = Connection Slough Treatment, ORC = Old River Control, ORT = Old River Treatment.

At each site, we sampled approximately 1 month before the herbicide treatment to ensure that we had pre-treatment data. We sampled each location again approximately 4 weeks post-treatment. We used this post-treatment lag-time to ensure that herbicide effects were as uniform as possible at each of the treatment sites. Since the control locations did not receive any herbicide treatment, we describe them in terms of before and after the treatment date to indicate the point in time when herbicides were applied at comparable treatment locations. CDBW staff collected water-quality measures throughout the treatment season in accordance with National Pollution Discharge Elimination System (NPDES) permitting requirements (CDBW 2012) using a Hach HQ30 meter and Luminescent Dissolved Oxygen (LDO) probe for DO measures on the periphery of water hyacinth mats. The CDBW collected DO measures only in areas where they sprayed herbicides (see Appendix A, Table A1 for sampling dates and associated DO measures).

For each sampling event, we used a numbered grid overlaid on a graphical representation of each weed mat, and a random number generator to select four portions of the mat to sample. We collected four random samples of water hyacinth and associated invertebrates per site using a custom-built ¼-m^2 quadrat with a 200-µm mesh pouch (~0.6 m deep). For each sampling event, we scooped the sampler into the water column beneath the water hyacinth mat then brought the sampler upward, through the mat. This approach allowed us to sample the water column, the epiphytic invertebrates found on the water hyacinth roots, and those on above-water plant structures. In the field, we rinsed invertebrates from the interior of the mesh as well as from the plant material. We bagged the rinsed water hyacinth, preserved the invertebrates in 70% ethanol, and transported them to the laboratory for processing.

Laboratory Procedures

In the laboratory, we dried water hyacinth material at 60°C (until constant weight), and we recorded dry plant biomass. In our sub-sampling protocol for invertebrates, we sorted the invertebrates by size class by rinsing them through stacked sieves (No. 10 [2 mm], No. 18 [1 mm], No. 35 [500 µm], and No. 50 [297 µm]). We completely counted all invertebrates ≥ 1 mm. We transferred invertebrates < 1 mm to a pan and evenly distributed them across a numbered grid. Using a random number generator, we selected 10 grid cells, using a pipette to extract the contents of those cells. We counted and identified invertebrates to genus, then extrapolated total sample numbers from sub-sample counts.

Statistical Analyses

To assess differences in invertebrate abundance, we natural-log transformed the data to achieve normality, and compared invertebrate abundance per gram plant biomass before and after treatment, as well as treatment versus control locations using mixed effects generalized linear models (GLMMs), with bootstrapped confidence intervals (R package "lme4"; Bates et al. 2016). We chose to analyze the invertebrate abundance per gram plant biomass because other studies have shown that increased macrophyte biomass can support higher densities of invertebrates (Schultz and Dibble 2012). This allowed us to control for differences in water hyacinth biomass between sites and sampling dates to detect differences from herbicide treatment. We used the same method of GLMMs to test whether plant biomass changed before and after treatment, and at control versus treated sites. To see whether invertebrates per ¼-m^2 quadrat of water surface area were affected by the combination of herbicide and change in plant biomass, we compared invertebrates per sample using GLMMs as well.

To determine whether particular taxa were affected differentially, we used GLMMs to perform univariate comparisons of taxa-specific abundance before and after treatment, in addition to control and treatment locations. We also divided the sampled invertebrates into categories, including zooplankton, gill-breathing arthropods, air-breathing arthropods, and mollusks; and used GLMMs to assess any differences in trait- and size-groups. All p-values were judged significant based on Tukey–Kramer honestly significant difference (HSD) test for multiple post-hoc comparisons.

To assess differences in invertebrate communities, we tested for overall differences in community composition using permutational multivariate analysis of variance (PERMANOVA; function "adonis" in R package "vegan" Oksanen et al. 2016). We performed non-metric, multi-dimensional scaling ordination (NMDS; function "metaMDS" from R package "vegan"; Oksanen et al. 2016) to visually display differences in invertebrate community diversity. We then used GLMMs to compare the following: average richness (measured as the average number of taxa collected at each sampling event) and average percent dominant taxa (measured as the average maximum number of individuals within a taxa divided by the average total number of taxa found at each sampling event). To further evaluate potential differences in invertebrate communities, we compared diversity indices among times and treatment, including Jaccard Index (Equation 1) and Sorenson's Coefficient of Community Similarity (Brower et al. 1998) (Equation 2).

Equation 1 Jaccard Index

$$J(A,B)=\frac{|A\cap B|}{|A\cup B|}=\frac{|A\cap B|}{|A|+|B|-|A\cap B|} \tag{1}$$

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Table 1 Terms, model estimates, standard errors, and confidence intervals for generalized linear mixed models with the formula [Response ~ Before/After + Control/Treatment + Error(Location)] where the responses are total plant biomass, invertebrates per gram plant biomass, and total invertebrate abundance

Response variable	Term	Estimate	Std. Error	df	*t*-value	*p*–value	2.50%	97.50%
Plant biomass	Intercept	43.962	6.111	12.15	7.19	<0.005	31.956	55.967
	Before/ After	–6.915	6.681	72.04	–1.04	0.304	–19.854	6.150
	Treatment/ Control	21.970	6.592	71.99	3.33	0.001	9.147	34.792
	Interaction	–22.329	9.337	72.08	–2.39	0.019	–40.624	–4.273
Inverts per gram plant biomass	Intercept	2.113	0.274	9.55	7.70	<0.005	1.567	2.660
	Before/ After	–0.116	0.272	72.03	–0.43	0.672	–0.647	0.412
	Treatment/ Control	–0.038	0.268	71.99	–0.14	0.889	–0.560	0.484
	Interaction	0.219	0.380	72.06	0.58	0.566	–0.517	0.963
Total invertebrate abundance	Intercept	5.497	0.167	27.75	32.83	<0.005	5.176	5.818
	Before/ After	0.213	0.221	72.00	0.96	0.339	–0.217	0.642
	Treatment/ Control	0.219	0.221	72.00	0.99	0.324	–0.210	0.649
	Interaction	0.257	0.312	72.00	0.82	0.414	–0.351	0.864

Equation 2 Sorenson's Coefficient of Community Similarity

$$QS = \frac{2|X \cap Y|}{|X| + |Y|} \tag{2}$$

RESULTS

Plant Biomass and Invertebrate Abundance

On average, there was 22.0 g (SE = 6.60) more plant biomass per sample at the treated sites than at the control sites ($p = 0.001$; Table 1, Figure 2). The effect of time alone was small and not significant, with only 6.9 g (SE = 6.68) less plant biomass on average in the early-season samples relative to the late-season samples ($p = 0.304$, Table 1). The modeled interaction between time and treatment showed that there was 22.3 g (SE = 9.34) more biomass per sample at treatment locations in the late-season samples (p=0.019; Table 1, Figure 2). Plant biomass from treated sites included fragmented, dead, and dying material as well as the remaining portions of living plants. Fragmented pieces of dead and dying water hyacinth accumulated in layers as a result of wind and tidal action, which may partially account for this surprising finding.

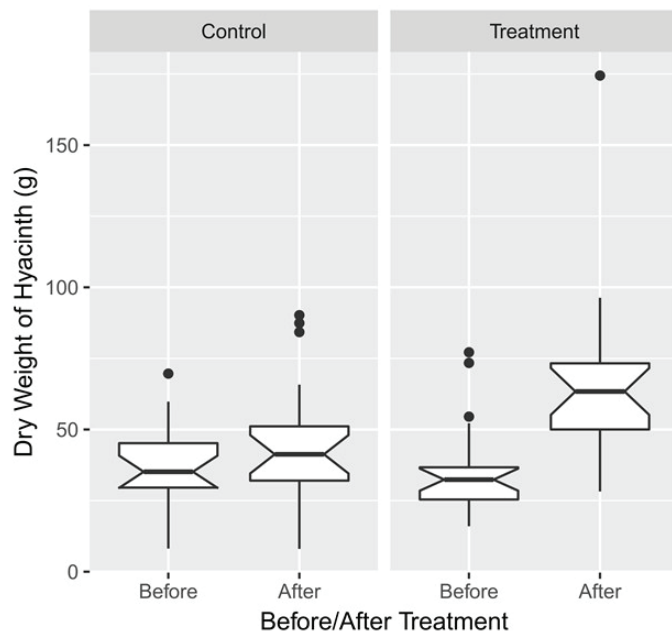

Figure 2 Box plot of mass of dried water hyacinth (in grams) before and after treatment for control and treatment groups. Notches within each box represent 95% confidence interval for comparing medians. GLMMs indicate significantly higher biomass for the "After" group, with a greater increase in biomass in the "Treatment" relative to the control group (see Table 1).

There were upward trends in invertebrate abundance in the late-season samples, but not significantly more invertebrates overall, or per gram plant biomass (Table 1: GLMM, time effect [$p = 0.672$], treatment effect [$p = 0.889$], and interaction effects [$p = 0.566$]; Figure 3A, 3B).

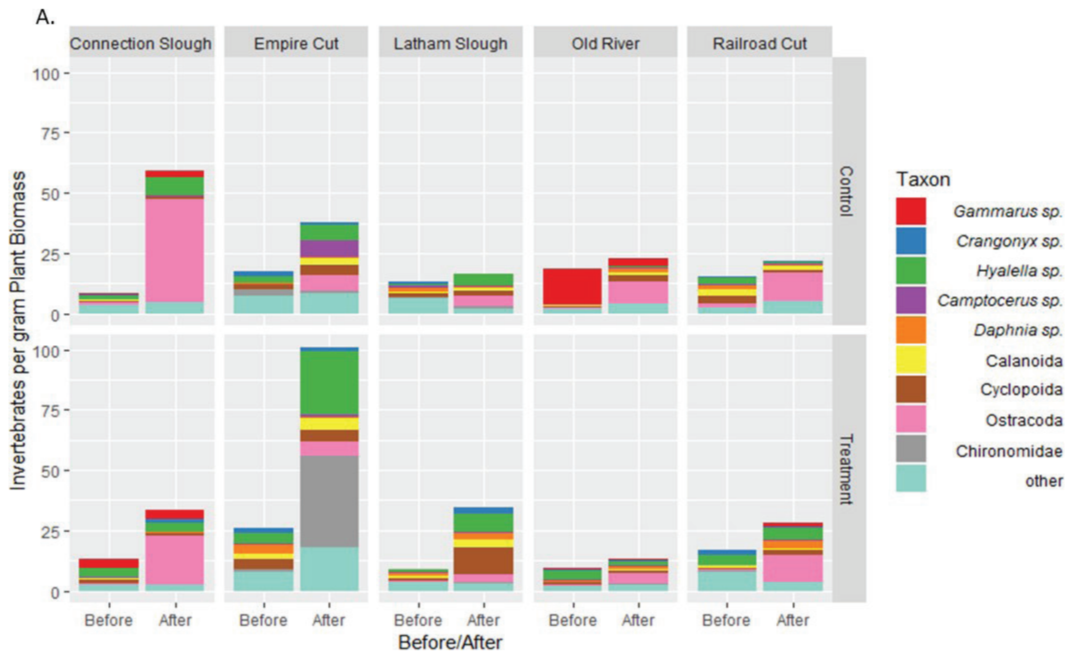

Figure 3A Invertebrates/(g) plant biomass for all regions combined, separated by treatment. The most common taxa are indicated by different colors, with all less common taxa grouped into the "other" category.

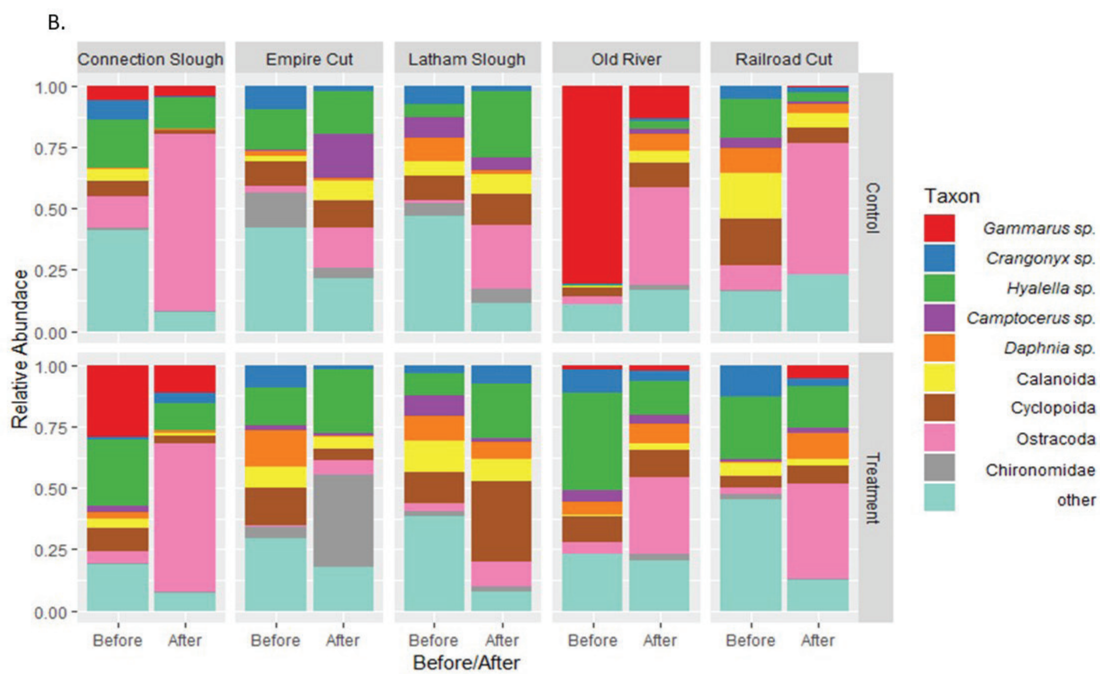

Figure 3B Relative abundance for all regions combined, separated by treatment. The most common taxa are indicated by different colors, with all less common taxa grouped into the "other" category.

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Invertebrate Richness and Diversity Measures

Average invertebrate richness was generally the same or only slightly greater after treatment dates at both the treatment and control locations. GLMMs indicate that there was no significant difference in richness between control and treatment locations ($F_{3,16} = 1.6324$, $p < 0.2705$) or for before versus after the treatment date at the sites that were treated with herbicide ($F_{3,16} = 6.1326$, $p < 0.0685$). Time x treatment effects were also not significant ($F_{3,16} = p < 0.9092$) (Figure 4).

There were no significant differences in the average percent dominant taxa between control and treatment locations ($F_{3,16} = 0.6977$, $p < 0.4506$), for before and after the treatment date at treated sites ($F_{3,16} = 1.0242$, $p < 0.3688$), or any detectable time x treatment interaction ($F_{3,16} = -0.0843$, $p < 0.7859$) (Figure 5).

PERMANOVA analysis of overall change in community structure did find a difference in the communities later in the season, though there was no difference between the control and treatment sites (PERMANOVA, $F_{1,19} = 4.798$, $p = 0.001$; Table 2). However, Jaccard index measures indicate that all locations were relatively uniform in their percent similarity before and after the treatment date (Table 3). All treatment locations had 55% to 67% Jaccard index similarity before and after treatment. All control locations had Jaccard index values between 41% and 67%, indicating slightly less but comparable levels of similarity before and after the treatment date. Sorenson's Coefficient of Community Similarity values for treatment locations ranged from 61 to 100 and 35 to 100 for control locations. These values indicate a high degree of overlap at the treatment locations before and after treatment (Table 3).

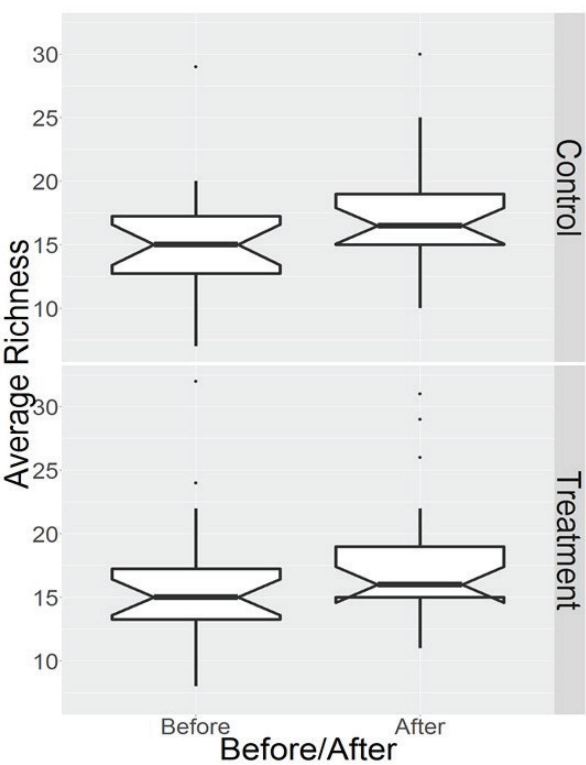

Figure 4 Distribution of average taxonomic richness for all regions combined, separated by treatment. Boxes with overlapping notches indicate no significant difference.

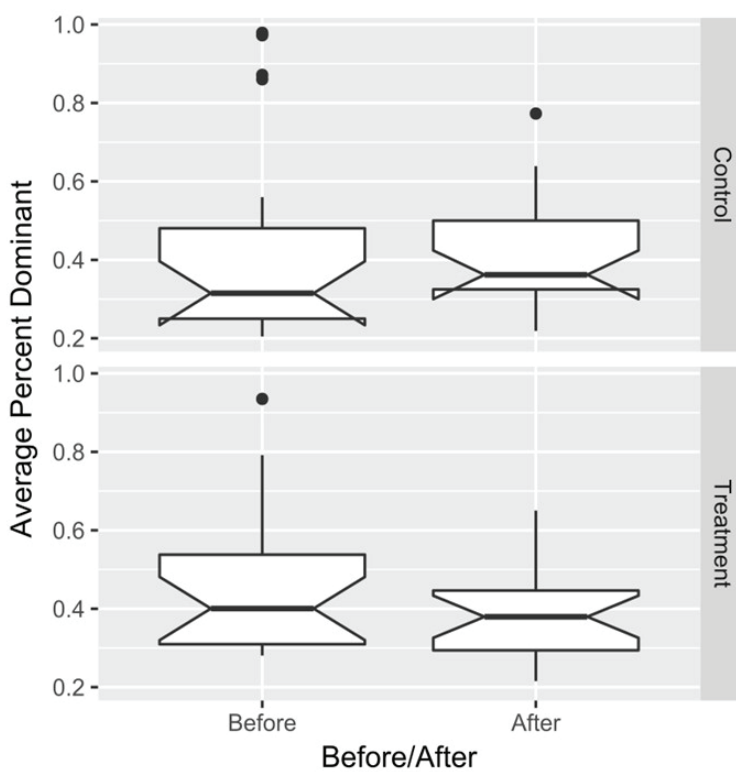

Figure 5 Average percent of community made up of the dominant taxon before and after treatment, separated by treatment type. Boxes with overlapping notches indicate no significant difference.

Table 2 Results of Permutational Multivariate Analysis of Variance (PERMANOVA)

Term	df	Sums of Sqs	Mean Sqs	*f*–value	R^2	*p*–value
Treatment/ Control	1	0.119	0.119	0.761	0.034	0.690
Before/After	1	0.752	0.752	4.798	0.213	0.001
Residuals	17	2.664	0.157		0.754	
Total	19	3.535			1	

Table 3 Diversity measures at each location. Measures represent relative similarity before versus after the treatment date.

Location	Control/Treatment	Jaccard coefficient	Sorenson's coefficient
Connection Slough	Treatment	55	92
Connection Slough	Control	67	40
Empire Cut	Treatment	67	80
Empire Cut	Control	58	35
Latham Slough	Treatment	57	61
Latham Slough	Control	50	100
Old River	Treatment	67	100
Old River	Control	41	82
Railroad Cut	Treatment	59	71
Railroad Cut	Control	61	67

Invertebrate Community Analysis

NMDS ordination did not separate the samples taken at control locations from those taken at treatment locations. However, it did separate the samples taken before versus after the treatment date. The lack of separation of the invertebrate communities found at these locations indicates stronger similarities between locations than between time points in NMDS space (Figure 6A, 6B), and this conclusion is further supported by the PERMANOVA results (Table 2).

Univariate Analyses of Specific Taxa

The most common and abundant taxa at all locations included Amphipoda (*Gammarus* spp., *Hyalella* spp., *Crangonyx* spp.), Cladocera (*Camptocercus* spp., *Daphnia* spp.), Copepods (orders Calanoida and Cyclopoida), Ostracoda and Chironomidae. GLMMs indicate that on average, there were ~10 (SE = 1.34) more ostracods per gram plant biomass in the samples taken after the treatment date compared to those taken before the treatment date ($p < 0.0001$, Table 4). However, for all other taxa, there were no significant differences in abundance for samples before versus after the treatment date, samples taken at control versus treatment locations, or the time x treatment interaction (Table 4).

Less abundant, but functionally important taxa found at all locations included a weevil introduced as a biological control agent (*Neochetina bruchi*, [Warner]), several species of mollusk (*Gyraulus* sp., *Physella* sp., *Planorbella* sp.), mayflies in the family Baetidae, and several predacious arthropods (Belostomatidae, Zygoptera, Aranae). GLMMs indicate that of these taxa, *Planorbella* sp., Zygoptera and *N. bruchi* abundances were significantly greater later in the season ($F_{3,16} = 8.7520$, $p < 0.0092$; $F_{3,16} = 48.8589$, $p < 0.0001$; and $F_{3,16} = 6.8654$, $p < 0.0186$, respectively) and there were no differences between control and treatment locations for these taxa. Spiders had significantly greater abundance after treatment at the treatment location only ($F_{1,8} = 8.5716$, $p < 0.0191$). In combination, these taxa account for approximately 5% of the "other" bar in Figure 3A, 3B. GLMMS for functional groups categorized by size and respiratory mode (see Appendix A, Table A2 for a taxa list) revealed that there were ~14 more zooplankton invertebrates (SE = 1.44, $p = 0.002$) and ~14 more mollusks (SE = 1.38, $p = 0.027$) per gram plant biomass in the late-season samples than in the samples taken earlier in the season (Table 5). However, there were no significant differences for control versus treatment locations, nor for the interaction of time and treatment for these taxa.

DISCUSSION

Plant Biomass and Invertebrate Abundance

On average, we observed increased plant biomass per sample at both the control and the treatment locations in the late-season samples. The increase in biomass at treatment locations likely occurred because some plant material persists in growing between decomposing treated strips. The growing plant material condenses the dying material, which results in vertical layers of dead, dying, and living water hyacinth. Additionally, as treated water hyacinth's structural elements degrade, wind and

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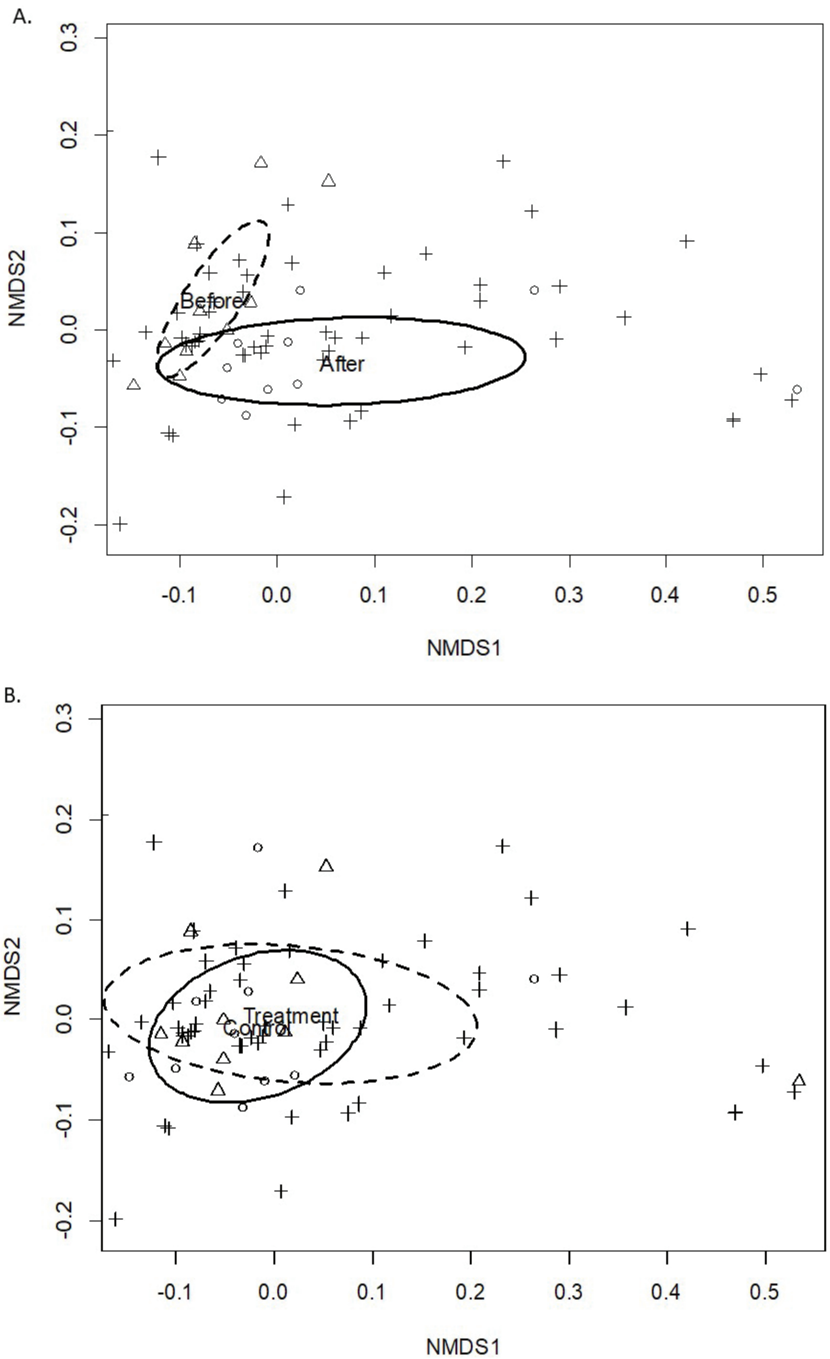

Figure 6 (**A**) Non-metric multi-dimensional scaling of community composition data. Crosses represent species scores. Triangles represent samples in the "Before" group while circles represent samples in the "After" group. The solid line circles the centroid of the Before samples and the dotted line circles the centroid of the After samples. (**B**) Non-metric multi-dimensional scaling of community composition data. Crosses represent species scores. Triangles represent samples in the "Treatment" group while circles represent samples in the "Control" group. The solid line circles the centroid of the Treatment samples and the dotted line circles the centroid of the Control samples.

tidal action can crowd plant fragments together in the mats, making them denser in fibrous material. Given that annual aquatic macrophytes typically experience a seasonal peak in plant biomass in the mid- to late-summer (June to September in California, USA; Westlake 1965) and that our after-treatment samples were taken between June and August, it is not particularly surprising that the after-treatment samples had higher biomass. Subsequent assessments of water hyacinth coverage in the Delta have shown variable trends between years. For example, using Landsat imaging and the Water Hyacinth Mapper Tool, scientists from NASA–Ames reported a 32% decline in 2017 annual peak acreage covered with floating aquatic vegetation compared

Table 4 Terms, model estimates, standard errors, and confidence intervals for generalized linear mixed models with the formula [Response ~ Before/After + Control/Treatment + Error(Location)] where the responses are natural log-transformed abundance for the most common and abundant taxa

Taxon	Term	Estimate	Std. Error	df	*t*–value	*p*–value	2.50%	97.50%
Calanoid Copepods	Intercept	–0.711	0.536	9.29	–1.326	0.217	–1.768	0.300
	Before/After	0.777	0.541	12.00	1.435	0.177	–0.271	1.853
	Treatment/Control	0.251	0.541	12.00	0.463	0.651	–0.691	1.221
	Interaction	–0.309	0.766	12.00	–0.403	0.694	–1.665	1.120
Camptocercus	Intercept	–2.399	0.692	14.32	–3.465	0.00368	–3.715	–1.055
	Before/After	1.843	0.877	12.00	2.102	0.05736	0.136	3.540
	Treatment/Control	1.454	0.877	12.00	1.658	0.12318	–0.247	3.247
	Interaction	–2.054	1.240	12.00	–1.657	0.12349	–4.523	0.462
Chironomids	Intercept	–1.635	0.852	7.32	–1.918	0.0947	–3.332	0.003
	Before/After	0.452	0.734	12.00	0.616	0.5496	–1.023	1.938
	Treatment/Control	–0.457	0.734	12.00	–0.623	0.545	–1.894	1.071
	Interaction	1.470	1.038	12.00	1.415	0.1824	–0.644	3.449
Crangonyx	Intercept	–0.690	0.453	13.90	–1.522	0.15	–1.710	0.172
	Before/After	–0.246	0.564	12.00	–0.436	0.671	–1.510	0.829
	Treatment/Control	0.367	0.564	12.00	0.651	0.527	–0.724	1.554
	Interaction	0.772	0.798	12.00	0.967	0.353	–0.792	2.446
Cyclopoid Copepods	Intercept	0.161	0.334	10.85	0.482	0.639	–0.452	0.868
	Before/After	0.465	0.366	12.00	1.268	0.229	–0.250	1.158
	Treatment/Control	0.113	0.366	12.00	0.308	0.763	–0.701	0.781
	Interaction	0.297	0.518	12.00	0.574	0.577	–0.695	1.353
Daphnia spp.	Intercept	–1.461	0.679	15.99	–2.151	0.0471	–2.847	–0.120
	Before/After	0.558	0.956	12.00	0.584	0.57	–1.296	2.385
	Treatment/Control	0.560	0.956	12.00	0.586	0.5689	–1.215	2.335
	Interaction	0.506	1.352	12.00	0.374	0.7148	–2.295	3.072
Gammarus spp.	Intercept	–1.876	1.115	6.90	–1.683	0.137	–3.934	0.488
	Before/After	0.262	0.915	12.00	0.286	0.78	–1.590	1.934
	Treatment/Control	–0.596	0.915	12.00	–0.651	0.527	–2.282	1.110
	Interaction	0.824	1.295	12.00	0.636	0.536	–1.551	3.339
Hyalella spp.	Intercept	–0.001	0.477	11.89	–0.001	0.9988	–0.872	0.972
	Before/After	0.981	0.549	12.00	1.789	0.0989	0.059	2.095
	Treatment/Control	1.036	0.549	12.00	1.889	0.0833	0.030	2.037
	Interaction	–0.262	0.776	12.00	–0.337	0.7417	–1.818	1.202
Ostracoda	Intercept	–0.586	0.369	6.71	–1.59	0.158	–1.309	0.112
	Before/After	2.928	0.295	12.00	9.913	3.94E-07	2.368	3.535
	Treatment/Control	–0.423	0.295	12.00	–1.431	0.178	–0.999	0.241
	Interaction	0.035	0.418	12.00	0.084	0.934	–0.796	0.876

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Table 5 Terms, model estimates, standard errors, and confidence intervals for generalized linear mixed models with the formula [Response ~ Before/After + Control/Treatment + Error(Location)] where the responses are natural log-transformed abundance for the most invertebrate functional groups categorized by size and respiratory mode.

Functional group	Term	Estimate	Std. Error	df	*t*–value	*p*–value	2.50%	97.50%
Gill breathers	Intercept	1.729	0.373	15.21	4.643	0.000	1.018	2.486
	Before/After	– 0.143	0.491	12.00	– 0.292	0.775	– 1.018	0.921
	Treatment/Control	0.686	0.491	12.00	1.398	0.187	– 0.301	1.683
	Interaction	– 0.686	0.694	12.00	– 0.988	0.342	– 2.212	0.652
Air breathers	Intercept	– 1.609	0.131	16.00	– 12.299	0.000	– 1.871	– 1.373
	Before/After	– 0.045	0.185	16.00	– 0.243	0.811	– 0.397	0.297
	Treatment/Control	0.257	0.185	16.00	1.390	0.184	– 0.104	0.628
	Interaction	– 0.365	0.262	16.00	– 1.395	0.182	– 0.854	0.131
Zooplankton	Intercept	2.917	0.279	14.81	10.439	0.000	2.397	3.459
	Before/After	– 1.435	0.361	12.00	– 3.970	0.002	– 2.165	– 0.741
	Treatment/Control	– 0.125	0.361	12.00	– 0.347	0.734	– 0.910	0.604
	Interaction	0.100	0.511	12.00	0.195	0.849	– 0.940	1.144
Mollusks	Intercept	3.219	0.246	14.96	13.096	0.000	2.672	3.669
	Before/After	– 0.809	0.320	12.00	– 2.528	0.027	– 1.444	– 0.144
	Treatment/Control	0.188	0.320	12.00	0.586	0.569	– 0.437	0.848
	Interaction	– 0.279	0.453	12.00	– 0.617	0.549	– 1.287	0.607

with 2015 values (Hard 2018). However, provisional 2019 data from the same source indicates an increase in water hyacinth (and water primrose) acreage compared with values at the same time in 2018 (Potter 2015). Longer-term studies are needed to assess overall WHCP effectiveness.

In general, we observed more invertebrates per gram plant biomass after the treatment date, though these results were not significant. This increase can likely be attributed to several cumulative influences. For example, as discussed above, more dense plant mats can provide increased surface area for epiphytic invertebrate colonization. Also, several studies indicate strong seasonal differences in aquatic invertebrate abundance (i.e., Peterson and Vayssieres 2010; Thompson et al. 2013; Young et al. 2016), with higher abundance occurring during the summer dry season in Mediterranean climate regions (Gasith and Resh 1999; Beche et al. 2006; Resh et al. 2013) like the Delta. Therefore, it is likely that the increase in plant biomass as well as invertebrate density is a function of season and plant/invertebrate phenology. This increase in invertebrate abundance may help provide food resources for native fishes, particularly given the high abundance of highly nutritious amphipods and insects found in our samples (Tiffan et al. 2014). Since food limitation is considered a factor in many native fish declines in the Delta (Brown et al. 2016), finding slightly higher invertebrate abundance in the late-season samples is an encouraging sign for adaptive management efforts that balance ecosystem productivity with water hyacinth control.

Invertebrate Richness and Diversity Measures

We did not observe a difference in richness or percent dominant taxa between control and treatment sites before versus after the treatment date. If there were treatment effects, we would expect to also see differences in the members of the invertebrate community—i.e., taxa that are more tolerant of low oxygen, or more detritivores. However, our lack of evidence for such community differences, and the observed similarities in Jaccard Index and Soreson's Coefficient of Community Similarity, lead us to conclude that any treatment effects are not great enough to significantly alter the invertebrate community richness or dominance measures.

The lack of hull separation in NMDS ordination for control and treatment locations, and the lack of significant PERMANOVA results for control versus treatment, further strengthens our finding that the aquatic invertebrate communities sampled in water hyacinth are largely similar between control and treatment locations. However, non-significant phenological differences exist in community composition before versus after the treatment date, particularly for invertebrate abundance.

Taxa-Specific Populations

Of the most common and abundant taxa, ostracods are the only taxa for which abundance was significantly greater after the treatment date. Their increased relative abundance is likely a seasonally driven phenomenon (Peterson and Vayssieres 2010; Resh et al. 2013; Corline et al. 2017).

Planorbella spp., Zygoptera nymphs, and *N. bruchi* are functionally important taxa that were generally rare relative to many other observed taxa. As for ostracods, we observed significant increases in abundance for these taxa after the treatment date that were likely normal seasonal increases.

Zygoptera have been reported to play an important role as forage for fish in other systems (Power 1992), and both living and decaying water hyacinth provided habitat for them. Spiders had significantly greater abundance after treatment at the treatment locations only. They are voracious predators of emerging aquatic insects, and, along with damselflies, may also be a predator of the *N. bruchi* weevils that currently serve as biological control agents of water hyacinth.

Functional Categories of Invertebrates

The significant increase in zooplankton abundance after treatment was likely driven by the large relative increase in ostracods found later in the season, as described above. Mollusk populations may have also increased in the late-season as a result of phenological changes, or as a result of potentially increased biofilms as a by-product of plant decomposition. We did not observe significant differences in abundance for gill-breathers or air-breathers (see Appendix A, Table A2).

CONCLUSIONS AND IMPLICATIONS

Through our case study, we assessed whether current control efforts for invasive water hyacinth in the Delta affect invertebrate communities that use water hyacinth as habitat. The results of this study provide valuable insight into the little-examined transition phase between the herbicide application and open-water phases of water hyacinth management. We concluded that current management efforts for invasive water hyacinth using glyphosate do not affect invertebrate abundance or diversity during a month-long, post-treatment period of decay.

Our results demonstrated that zooplankton and macroinvertebrate communities clearly continue to use herbicide-treated water hyacinth mats as habitat even when the vegetation is dead or dying. The observed late-season increase in damselflies is ecologically meaningful because they serve a dual role in aquatic food webs—that of predator and prey—and may be particularly attractive to foraging Delta fish species later in the season. More generally, the decaying water hyacinth plants may provide a resource pulse or temporary subsidy for fish, because as the plants begin to sink, and root structures degrade, the epiphytic invertebrates disperse and are much easier to prey upon when they lack the protective cover of submerged roots (Padial et al. 2009). Concentration of prey can result in increased strike success and reduced search time for fish (Ware 1972). Future research is needed to determine the degree to which fish are foraging in and/or near water hyacinth mats, what happens with invertebrate dispersal after herbicide-induced plant decomposition, and if/how fish foraging behavior changes as a result.

If we had collected the late-season samples much later than 4 weeks post-treatment, it is likely that we would have encountered different circumstances. For example, herbicide-treated vegetation continues to decompose and eventually sinks, leaving open water in its place—and pelagic areas without macrophytes are comparatively depauperate in macroinvertebrate abundance (Durand 2015). However, since the CDBW's herbicide applications are spaced temporally

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and geographically throughout the growing season, weed mats senesce and sink in a mosaic fashion, which may allow invertebrates to move between habitat patches. Additionally, if we had selected sites across a salinity gradient or across changing hydrodynamic circumstances, we might have encountered different findings—in terms of initial invertebrate community composition, behavior of weed mats during the study, and community responses to herbicides. Finally, it is important to note that this study took place during the last year of a 5-year drought. In a non-drought year, flows from winter storms would have likely washed away more water hyacinth weed mats, resulting in lower spring and summer weed biomass. Because higher macrophyte biomass is generally correlated with higher invertebrate abundance, it is possible that we would have observed relatively lower invertebrate abundance in a non-drought year. However, we do not have reason to believe that the overall patterns we observed would necessarily be different in a non-drought year. Future research with longer time horizons would also be beneficial in informing the CDBW's current adaptive management efforts in the Delta. For example, it would be advantageous to determine how invertebrate communities might respond to herbicide treatment as macrophyte community composition changes over time (possibly through restoration activities), how longer-term changes in hydrologic regimes might affect the outcomes of herbicide treatment and the composition of invertebrate communities that use the target weed as habitat, and how macrophyte mat-dwelling invertebrates may become available to fishes.

In the absence of the abundant littoral habitats that were once characteristic of the Delta ecosystem, invertebrates that are crucial links in Delta food webs employ the habitats that are available—which includes water hyacinth because of its sheer abundance and Delta-wide distribution. However, water hyacinth mats are not necessarily optimal habitat for invertebrates. Nonetheless, aquatic invertebrates persist in water hyacinth beds in the physically altered and biologically invaded Delta. Given the urgent socio-economic and ecological need to manage water hyacinth invasions around the world, those leading such activities should carefully conduct control efforts in the context of adaptive management, and integrate water hyacinth control efforts with habitat-restoration efforts.

From a long-term perspective, if water hyacinth were eradicated without extensive restoration of native macrophytes Delta-wide, there would likely be consequences for invertebrates that use water hyacinth as habitat and also potentially serve as forage for local fishes. Many potential scenarios might result from water hyacinth eradication in the absence of other ecosystem restoration activities (e.g., changes in primary production in phytoplankton communities, colonization by other non-native submerged macrophytes, etc.) that are beyond the scope of this paper. Primarily, we desire to underscore the need for thoughtful and strategic restoration that is paired with invasive species control. In a cautionary example of the importance of such a pairing, managers in southwestern riparian ecosystems (USA) achieved success in controlling the invasive Salt Cedar (*Tamarix* spp.), only to discover that without combining control efforts with native vegetation restoration, the endangered Southwestern Willow Fly Catcher (*Empidonax traillii extimus*) struggled to locate nesting habitat (Bateman et al. 2010).

There are many impediments to effective adaptive management in the Delta, including a general trend of managers' failure to evaluate and synthesize management results (Delta ISB 2016). However, the present case study is an example of state and federal agency employees collaborating with academic researchers to address this common pitfall by evaluating the results of management operations and incorporating the evidence into decision-making about future management activities. More broadly, we hope this case study is a useful example for managers around the world who manage invasive species in the context of aquatic food webs.

AUTHORS' CONTRIBUTIONS

EDM conceived the ideas for the experiment. EDM, MP, PP, and SL designed the methodology; EDM and MP collected the data; EDM and RH analyzed the data. All authors contributed critically to the drafts and gave final approval for publication.

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