J. Aquat. Plant Manage. 59s: 33–40

Invasive aquatic weeds influence abundances of larval mosquitoes and other invertebrates

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ABSTRACT

Aquatic plants provide habitat structure that affects aquatic invertebrates. As invasive aquatic weeds, water hyacinth (*Eichhornia crassipes*) and Brazilian waterweed, aka egeria (*Egeria densa*) can modify and dominate aquatic habitats, altering natural ecosystems. Invasive aquatic vegetation could affect habitat quality for larval mosquitoes, a topic largely unexplored. Some aquatic weeds harbor mosquitoes, whereas others repress them. In this mesocosm study, we measured wild larval mosquito abundances and naturally recruited invertebrate predators and competitors in three aquatic habitat types: open water, water covered with water hyacinth, or water with egeria. Early in the development of weed populations (3 to 6 wk), we found more larval mosquitoes in open water than in other habitats. Abundance was 9-fold lower in water hyacinth and over 30-fold lower in egeria than in water tanks. Competitors were about five times more abundant in open water and egeria than in water hyacinth, and larvae of a representative competitor, Ceratopogonidae, had the same pattern but were over seven times more abundant. Later (Weeks 8 to 10), mosquitoes did not vary among treatments, whereas competitors were almost 3-fold lower in hyacinth than in open water. Predators were marginally lower with hyacinth both early and later ($P < 0.07$). Overall, healthy water hyacinth had comparatively low numbers of larval mosquitoes and competitors, and when compared to open water, egeria strongly suppressed mosquitoes but did not inhibit predators or competitors. The results have implications for targeting of sites for mosquito control in relation to aquatic weed invasions and integrating control strategies, according to One Health practices.

Key words: Brazilian waterweed, *Egeria densa*, *Eichhornia crassipes*, One Health, water hyacinth.

INTRODUCTION

Mosquitoes are implicated as leading causes of morbidity and mortality worldwide through their ability to vector pathogens that cause serious diseases, such as West Nile virus, onchocerciasis, and malaria (Goddard et al. 2003, Farajollahi et al. 2011, Rejmánkova et al. 2013). One key mosquito control strategy involves managing and reducing larval mosquito habitats, including the presence of aquatic plants (Rogers 1967, Lawler et al. 2007). Larval mosquitoes are affected by multiple biotic and abiotic factors in their environment (Rogers 1967, Merritt et al. 1992, Washburn 1995, Blaustein and Chase 2007, Silver 2008, Rejmánkova et al. 2013). The presence of vegetation, conspecifics, competitors, predators, and water conditions such as temperature and pH all come together to form dynamic larval mosquito habitats of varying quality (Merritt et al. 1992, Washburn 1995, Blaustein and Chase 2007, Silver 2008, Rejmánkova et al. 2013).

The intersection between weed and mosquito management provides the opportunity for collaboration between disciplines, exemplifying the concept of One Health (Grace 2014, Dente et al. 2019). To highlight the interdisciplinary aspect of this research further, we partnered with the U.S. Department of Agriculture's Delta Region Areawide Aquatic Weed Management Program (DRAAWP). By focusing on the potential role of aquatic weeds in mosquito habitat quality, we address concerns surrounding aquatic weed invasions for vector abatement districts in many regions, including in the Sacramento–San Joaquin Delta region of California, USA (Foss et al. 2015).

Vegetation plays a major role for determining habitat for some species of mosquitoes such as *Anopheles* spp. (Asmare et al. 2017, Wondwosen et al. 2017), but is largely unexplored for other key species, such as *Culex* mosquitoes (Rogers 1967, Silver 2008, Rejmánkova et al. 2013, Gettys et al. 2014), which can vector West Nile virus (Foss et al. 2015, Reisen and Wheeler 2016). Some invasive aquatic weeds harbor mosquitoes; others repress populations. To illustrate, wetlands with water lettuce (*Pistia stratiotes*) are preferred host sites for many mosquito species (Weldon and Blackburn 1967, Silver 2008), but eared water fern (*Salvinia auriculata*) represses larval mosquito populations by limiting access of gravid females to the water surface (Hobbs and Molina 1983). Water hyacinth (*Eichhornia crassipes*) is thought to suppress mosquitoes by creating habitat for larvivorous predators (Weed 1924, Ofulla et al. 2010), but researchers have also found positive associations between this weed and mosquito larvae (Minakawa et al. 2002, Silver 2008). Weed manipulation can be a key part of a mosquito abatement program. However, the full extent of aquatic weed interactions and larval mosquitoes are not well studied.

Aquatic plants, including some weedy species, may provide larval mosquitoes with refugia from predators (Hall 1972, Merritt et al. 1992, Day 2016). Dense aquatic plants may also reduce water movement, further protecting larval mosquitoes. Aquatic plants can also reduce oxygen avail-

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ability in the water, a deterrent to larval mosquito predators and competitors dependent on dissolved oxygen (Buscemi 1958, Flores and Carlson 2006). Additionally, plants are often a source of larval mosquito food, either through direct contribution of fine particulate organic matter by decay, or indirectly through promotion of bacteria and other microbial foodstuffs (Barber and Hayne 1925, Rozeboom 1935), which exude chemical cues that attract mosquitoes (Afify and Galizia 2015). Plants may indicate good larval habitat to adult females, and flowers may attract hungry adult mosquitoes of either sex seeking to feed on nectar (Blaustein and Kotler 1993). Some mosquitoes, including *Culex quinquefasciatus*, are attracted to exudates from water hyacinth roots (Turnipseed et al. 2018).

On the other hand, some aquatic plants may deter mosquitoes. They can block the water surface, preventing access to atmospheric oxygen to larvae, bar females from ovipositing, and shade the water. Shading may decrease algal growth, limiting larval food, and may also lower water temperature, which is known to slow mosquito larval mosquito development (Walton et al. 2013). Secondary plant metabolites may also deter mosquitoes (Reiskind et al. 2009). Aquatic plants can also attract predators, including fish, and competitors (Walton et al. 1990, Mokany and Shine 2002, Reiskind and Wilson 2004). These outcomes vary depending on plant characteristics. With multiple possible interactions, understanding and identifying the potential impacts of aquatic weeds on diverse mosquito larval habitat is important for vector control.

We focus on two invasive aquatic weeds selected for their contrasting morphology, and because they are known to dominate aquatic landscapes in the Sacramento–San Joaquin Delta (Bubenheim et al. 2021, Caudill et al. 2021, Madsen et al. 2021). *Eichhornia crassipes* (Martius) Solms-Laubach (water hyacinth) is a floating, thick-leaved, monoecious plant that forms very dense mats at the surface. Its showy blossoms caused it to be introduced as an ornamental plant. However, it can double in population in as little as 2 wk, through its ability to reproduce through stolons as well as seeds, and it is classified as one of the worst aquatic weeds in the world (Villamagna and Murphy 2010). *Egeria densa* L. (Brazilian waterweed, or egeria) is a rooted, submerged dioecious plant. It grows to the water surface in dense stands that easily clog irrigation water intakes and tangle boat propellers. This poses a huge problem, as egeria can easily reproduce through cuttings. These two weeds are both major invaders of aquatic habitats in the Sacramento–San Joaquin Delta of northern California (Ta et al. 2017), and in many other areas. They exemplify typical characteristics of problematic invasive weeds: quick growth, strong competitive effects, and dense monotypic areas. We tested whether they were likely to contribute to mosquito-related public health problems.

To answer this question, we designed a mesocosm study to measure larval mosquito abundance in three habitat types: open water and dense growth of either water hyacinth or egeria. Our null hypotheses were 1) larval mosquitoes would not vary in abundance between treatments, and 2) predators and competitor species would not vary between treatments.

MATERIALS AND METHODS

We created mesocosms in a field near Putah Creek in Davis, CA to quantify wild larval mosquito abundances in habitats with different invasive weeds. We used 35 1,325-L polyethylene tanks[1] to represent three habitat types: open water, *Eichhornia crassipes* (water hyacinth, referred to as "hyacinth"), and *Egeria densa* (Brazilian waterweed, referred to as "egeria"). Completion of mesocosm construction marked Week 0 of the experiment.

Mesocosm construction occurred during the 2.5 wk before the start of the experiment. During this time, we installed approximately 144 15-cm Euro Mum pots[2] in each tank, reaching approximately 85% bottom surface coverage. Pots were lined with newspaper[2] and contained a 3:1 sand-to-soil mixture substrate. The soil mixture[3] was one part redwood compost, one part coarse sand and turkey manure, one part peat moss; added to this mix was dolomite at a rate of 1.78 kg m^{-3}. We collected zooplankton from approximately 20 plankton tows conducted no more than 1 m deep from the Delta at Orwood Resort, Brentwood, CA, the same source as the water hyacinth and egeria. Concentrated zooplankton (110 ml) were added to each tank. While plants were being transplanted, we half-filled tanks with water from Sacramento's municipal water district.[4] At the beginning of the experiment, we fully filled tanks with local water from Putah Creek and refilled as needed because of evaporation. We applied petroleum jelly to the tank edge to prevent frogs or other vertebrates from entering the tanks.

We collected plants from the Delta region at Orwood Resort, Brentwood, CA. We rinsed all the plants with water in a greenhouse to remove unwanted organisms. All plants were then kept at minimum overnight in the greenhouse in small plastic pools of water to remove any remaining organisms and reduce transplantation stress before transferring them to outdoor mesocosm tanks. We added hyacinth to tanks to achieve approximately 90% surface coverage at start of the experiment. Hyacinth grew to 100% coverage during much of the experiment. We planted egeria in the substrate pots by cutting approximately 20-cm, unbranched segments and twisting paired lengths together. Four pairs of egeria sprigs were planted ~2.5 cm deep into each pot, resulting in approximately 1,150 cuttings of egeria per tank. Egeria also grew well during the experimental window, and it reached the water surface. Both weeds flowered at least once.

Fifteen tanks of open water and 10 tanks each of egeria and hyacinth were randomly arranged and blocked by tank color (Figure 1). We took dip samples of larval mosquitoes and other surface and near-surface dwelling arthropods over 10 wk (10 total; Weeks 1, 3 to 6, and 8 to 10). We did not sample in Week 2 to minimize disturbance during community establishment. Because of a concurrent experiment, we did not sample Week 7; half of the tanks were then devoted to this second experiment, resulting in five tanks per treatment in Weeks 8 through 10 (Portilla and Lawler, 2020).

Mosquito sampling consisted of 10 dips per tank, 5 dips centrally and 5 dips around tank edges using standard 350-ml mosquito dippers.[5] We stored samples at room temperature in 70 to 95% ethanol in plastic bags.[6] We added granular Bti[7] after each dip sampling to reduce the

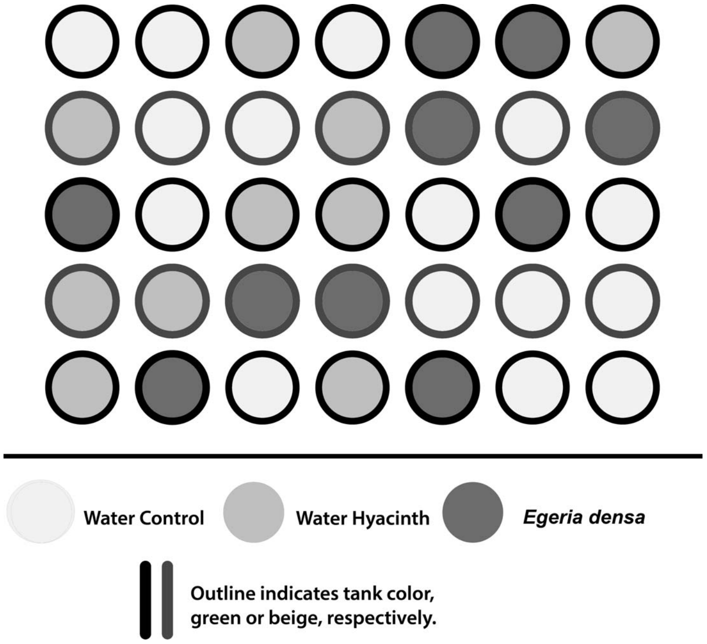

Figure 1. Randomized treatment layout of a mesocosm experiment with water hyacinth, egeria, and water-only tanks. Black circles represent green tanks ($N = 21$), and dark-gray circles represent beige tanks ($N = 14$). Each tank was 350-gallon (1,325 L) plastic tanks, blocked by color in rows, and contained similar substrate (3:1 sand:soil; see text for further information). Center color of circle represents treatment: the lightest gray represents open-water treatment ($N = 15$), center medium-tone gray represents presence of water hyacinth in water ($N = 10$), and the darkest center gray represents rooted egeria in water ($N = 10$). Key is below figure.

introduction of adult mosquitoes to the area. Bti quickly loses activity in the field in this formulation, within about 4 d (Becker et al. 1992, Van Essen and Hambree, 1982); thus we expected to observe new cohorts of mosquitoes each week.

We collected additional aquatic invertebrates every 2 wk (Weeks 3, 4, 6, 8, 10) via three sweeps along the bottom and side of the tanks with a stainless-steel sieve[8] with a diameter of 12.7 cm and 0.79-mm mesh size and stored them in 70 to 90% ethanol. Sweep samples were conducted within 1 d of dip samples. We took water quality measurements weekly with a multimeter[9] throughout the experiment (Weeks 1 and 3 to 10), including pH, dissolved oxygen, and temperature.

For nonmosquito invertebrates, we combined dip and sweep samples (both live and voucher samples) to increase sample size. Sweeps did not significantly contribute to mosquito numbers. Mosquitoes were sight-identified to at least genus level, and other macroinvertebrates were identified to order using light dissection microscopes.[10] We grouped invertebrates into one of three functional-trophic groups for analysis. These included mosquitoes (larvae and pupae), predators (Odonata larvae, aquatic Coleoptera, and aquatic Hemiptera), and competitors (Diptera larvae, Ephemeroptera larvae, and snails). No dipterans found were large enough to prey on mosquitoes. Ceratopogonidae (no-see-ums, or biting midges) are small omnivorous dipterans that are also of medical and veterinary concern (McCafferty 1981). We grouped these with "competitors," and we also analyzed them separately to assess if effects seen on mosquitoes were unique to mosquitoes, and not experienced by other small Diptera.

Analysis

We conducted analyses using Microsoft Excel[11], and JMP Data were divided into two periods: Early dates consisted of Weeks 3, 4, 5, and 6, $N = 10$ in hyacinth and egeria and $N = 15$ in open water tanks. Later dates consisted of Weeks 8 to 10, where $N = 5$ in all treatments.

Preliminary analysis revealed that Week 1 had comparatively low numbers of invertebrates and atypical and variable water quality measures, so we removed it from analysis, as this was still within the establishment window. We did not sample during Week 2 to avoid disturbing the recruitment process. We did not sample in Week 7 because of a concurrent experiment. To attain adequate numbers within each taxa for statistical analysis, we combined our data by averaging by tank within two time periods: early period (Weeks 3 through 6) and a later period (Weeks 8 through 10).

Using a quantile range test, we identified three outliers in mosquito data and three in Ceratopogonidae data, from individual tanks. There were no outliers in predators or competitors. The outliers appeared to be transients associated with tanks too close to either the flowering of a bush, or the placement of a small pool used to attract mosquitoes for a different study. We removed these outliers from subsequent analyses. Exploratory analysis showed that outlier removal did not affect which treatment contrasts were statistically significant. We also found three outliers in water quality measures; these were attributed to typos in original data sheets and removed from analysis.

We used a goodness-of-fit test and ran the Shapiro–Wilk method on residuals. As expected of count data, the distribution was not normal: we did not find an effective transformation, and variances were not equal.

We therefore ran nonparametric Kruskal–Wallis (KW) tests for each functional group by treatment to determine differences in abundances by habitat. We then ran *post hoc* nonparametric comparisons of treatment pairs. We used the Wilcoxon method and the more conservative Steel–Dwass method to correct for multiple comparisons. We show both kinds of *post hoc* tests to present a balance between Type I and Type II statistical errors.

RESULTS AND DISCUSSION

There were significant differences in the abundances of mosquitoes and other aquatic invertebrates between the three habitat types, especially early in the season (Table 1, Figure 2). The presence of conspecifics, competitors, predators, water conditions such as temperature and pH, as well as the presence and identity of vegetation all come together to produce larval mosquito habitats of varying quality (Merritt et al. 1992, Washburn 1995, Blaustein and Chase 2007, Silver 2008, Rejmánkova et al. 2013). Below we discuss how differences found in some of these factors may have affected mosquitoes.

Table 1. Statistics for abundances of aquatic macroinvertebrates in three mesocosm habitats. Kruskal–Wallis (KW) one-way chi-squared approximation (all df = 2), mean and standard deviation of mosquito, predator, competitor, and Ceratopogonidae abundances in two time periods across three treatments: open water, water hyacinth, and egeria, and pairwise comparisons for each treatment pair using Wilcoxon and Steel–Dwass methods.

Group, KW result	Week	Treatment 1	Mean	SD	Treatment 2	*Z*	Wilcoxon *P*	Steel–Dwass *P*
Mosquitoes	3–6	Water	88.500	53.579	*Egeria*	4.03	<0.0001	0.0002
	3–6	Hyacinth	9.050	5.977	Water	−3.58	0.0003	0.0010
$\chi^2 = 24.713$, $P < 0.001$	3–6	*Egeria*	2.820	2.288	Hyacinth	2.92	0.0035	0.0099
Competitors	3–6	Water	36.100	24.841	*Egeria*	0.22	0.8244	0.9732
	3–6	Hyacinth	6.750	3.694	Water	−3.91	<0.0001	0.0003
$\chi^2 = 19.073$, $P < 0.001$	3–6	Egeria	32.220	20.079	Hyacinth	−3.63	0.0003	0.0008
Ceratopogonidae	3–6	Water	3.060	2.855	*Egeria*	0.67	0.5038	0.7818
	3–6	Hyacinth	0.400	0.591	Water	−3.23	0.0012	0.0035
$\chi^2 = 9.565$, $P = 0.0084$	3–6	*Egeria*	3.140	4.404	Hyacinth	−1.66	0.0978	0.2226
Predators	3–6	Water	12.100	4.768	*Egeria*	−1.86	0.0628	0.1503
	3–6	Hyacinth	17.020	6.428	Water	2.05	0.0400	0.0997
$\chi^2 = 5.715$, P= 0.0574	3–6	*Egeria*	18.500	8.299	Hyacinth	−0.38	0.7052	0.9242
Mosquitoes	8–10	Water	3.800	3.329	*Egeria*	1.05	0.2948	0.5468
	8–10	Hyacinth	4.200	3.176	Water	0.00	1.0000	1.0000
$\chi^2 = 1.826$, $P = 0.4012$	8–10	*Egeria*	1.930	1.801	Hyacinth	1.05	0.2933	0.5448
Competitors	8–10	Water	24.860	15.161	*Egeria*	−1.88	0.0601	0.1445
	8–10	Hyacinth	9.330	6.695	Water	−1.89	0.0593	0.1428
$\chi^2 = 9.679$, $P = 0.0078$	8–10	*Egeria*	43.060	13.766	Hyacinth	−2.51	0.0119	0.0320
Ceratopogonidae	8–10	Water	0.460	0.869	*Egeria*	−1.62	0.1060	0.2386
	8–10	Hyacinth	1.000	2.054	Water	0.00	1.0000	1.0000
$\chi^2 = 3.779$, $P = 0.1511$	8–10	*Egeria*	3.400	2.670	Hyacinth	−1.40	0.1612	0.3404
Predators	8–10	Water	15.400	13.191	*Egeria*	−1.46	0.1437	0.3092
	8–10	Hyacinth	8.330	2.666	Water	−0.84	0.4034	0.6809
$\chi^2 = 5.580$, $P = 0.0614$	8–10	*Egeria*	29.330	15.993	Hyacinth	2.09	0.0367	0.0921

In Weeks 3 through 6, larval mosquito abundances were by far the highest in open water mesocosms, next highest in water hyacinth, and least abundant in egeria (Figure 2, Table 1). Mosquitoes were comparatively rare in tanks with either egeria or water hyacinth throughout the experiment, but differences were not significant in the later period (Figure 2). In Weeks 3 to 6, we found almost 10 times more mosquitoes in open water than in water hyacinth, and 30 times more mosquitoes in open water than in egeria (Table 1). Of 6,587 mosquitoes collected, over 95% were identified as the genus *Culex*. In Weeks 3 through 6, over 96% were identified to *Culex*, and 2.5% were identified as *Anopheles*. In the later period, *Culex* dropped to 89%, and *Anopheles* increased to 9.8%. The remainder in each period were

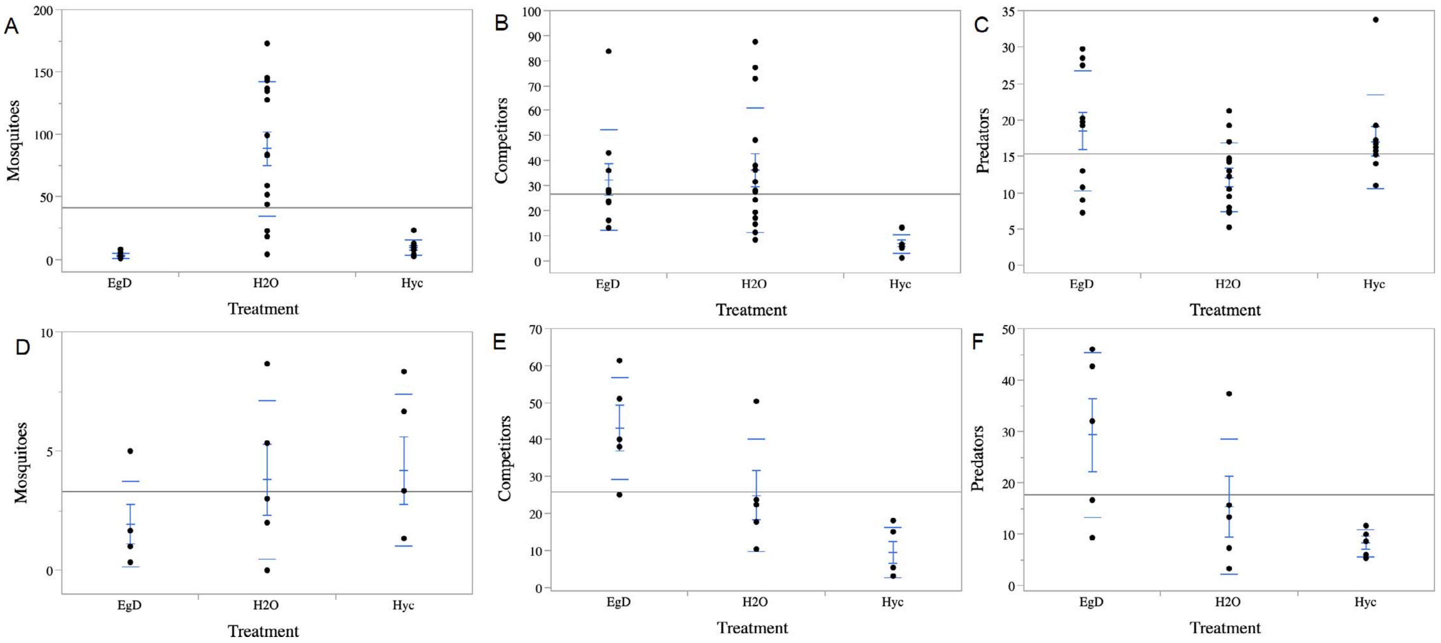

Figure 2. Macroinvertebrate abundances in three treatments in early (top row) and later time periods (bottom row). Treatments were three mesocosm habitats: water, hyacinth, and egeria. Mosquitoes: Weeks 3 through 6: A, Weeks 8 through 10: D; competitors: Weeks 3 through 6: B, Weeks 8 through 10: E; predators: Weeks 3 through 6: C, Weeks 8 through 10: F. Each point represents one tank sampled at one point in time during the specified time frame. Bars show mean ± SE.

Table 2. Statistics for water quality measures in three mesocosm habitats in early and later time periods. Kruskal–Wallis (KW) one-way chi-squared approximation (all df = 2), mean and standard deviation of pH, percent dissolved oxygen, and temperature (C°) in two time periods across three treatments: water, water hyacinth, and egeria, and pairwise comparisons for each treatment pair using Wilcoxon and Steel–Dwass methods.

Metric, KW result	Week	Treatment 1	Mean	Standard deviation	Treatment 2	Z	Wilcoxon *P*	Steel–Dwass *P*
pH	3–6	Water	8.836	0.267	*Egeria*	−3.97	<0.0001	0.0002
	3–6	Hyacinth	7.202	0.369	Water	−4.08	<0.0001	<0.0001
$\chi^2 = 28.829$, $P < 0.0001$	3–6	*Egeria*	9.492	0.265	Hyacinth	−3.75	0.0002	0.0005
Temperature (C)	3–6	Water	20.723	0.740	*Egeria*	−0.61	0.5417	0.8145
	3–6	Hyacinth	19.834	0.378	Water	−2.91	0.0036	0.0100
$\chi^2 = 14.182$, $P = 0.0008$	3–6	*Egeria*	20.870	0.399	Hyacinth	−3.59	0.0003	0.0010
% dissolved oxygen	3–6	Water	49.083	8.469	*Egeria*	−2.75	0.0060	0.0166
	3–6	Hyacinth	23.515	9.036	Water	−3.86	<.0001	<0.0003
$\chi^2 = 23.495$, $P < 0.0001$	3–6	*Egeria*	59.843	9.175	Hyacinth	−3.74	<.0001	<0.0005
pH	8–10	Water	9.170	0.344	*Egeria*	−1.67	0.0947	0.2163
	8–10	Hyacinth	7.270	0.032	Water	−2.51	0.0122	0.0326
$\chi^2 = 10.820$, $P = 0.0045$	8–10	*Egeria*	9.660	0.108	Hyacinth	−2.51	0.0122	0.0326
Temperature (C)	8–10	Water	23.160	0.272	*Egeria*	1.46	0.1437	0.3092
	8–10	Hyacinth	21.040	0.322	Water	−2.51	0.0122	0.0326
$\chi^2 = 10.500$, $P = 0.0052$	8–10	*Egeria*	22.790	0.295	Hyacinth	−2.51	0.0122	0.0326
% dissolved oxygen	8–10	Water	44.380	9.690	*Egeria*	−1.25	0.2101	0.4218
	8–10	Hyacinth	11.173	1.028	Water	−2.51	0.0122	0.0326
$\chi^2 = 10.220$, $P = 0.006$	8–10	*Egeria*	53.813	3.003	Hyacinth	−2.51	0.0122	0.0326

either pupae, or too small or damaged to identify accurately. Identifying *Culex* mosquitoes is of particular public health importance because they are the major vector of West Nile virus and other viruses that can cause encephalitis in humans and in wild and domestic animals (Foss et al. 2015, Reisen and Wheeler 2016). To our knowledge this is the first study to show that egeria potentially inhibits mosquitoes, but the mechanism is unknown. Egeria would not have shaded the water as much as water hyacinth. However, egeria may inhibit some phytoplankton through allelopathy (Vanderstukken et al. 2011), which is an important resource for mosquito larvae (Becker et al. 2010). More research is needed to understand effects of egeria on mosquitoes. There were no treatment differences in mosquito abundance in the late weeks (8 to 10) (Table 1), when mosquitoes were in general less abundant, and when we had fewer replicates with which to detect effects.

Competitors were mostly in the insect orders Ephemeroptera, Diptera, and in the Phylum Gastropoda. Unlike larval mosquitoes, these were similarly common in open water and in egeria tanks throughout the experiment and were least common in water hyacinth tanks (Figure 2, Table 1). Therefore, mosquito abundances did not seem to be influenced much by competitors. The pattern observed in larval mosquito abundance was also dissimilar to larvae of Ceratopogonidae, which are dipteran larvae similar in size to mosquito larvae. These were common in samples (12.6% of all Diptera), and followed the same pattern as competitors in general, with similar abundances in water and egeria, and lower abundance in hyacinth tanks in the early weeks (Table 1).

Differences in diet between mosquitoes and competitors might have caused these disparate responses to egeria and hyacinth. Both kinds of weeds can compete with phytoplankton, a major resource for filter-feeding mosquito larvae, through shading, nutrient uptake, and possibly allelopathy (McVea and Boyd 1975, Shanab et al. 2010, Vanderstukken et al. 2011). Although both mosquitoes and their competitors feed on detritus and browse on surfaces, the other competitors do not filter-feed like mosquitoes, relying more heavily on attached or filamentous algae and detritus (McCafferty 1981, Merritt et al. 2008). Ceratopogonids are omnivorous (Merritt et al. 2008), and these may have been less limited by any negative effects of egeria or water hyacinth on phytoplankton. We acknowledge that in flowing sloughs, water hyacinth does provide habitat for a variety of zooplankton and other invertebrates (Donley Marineau et al. 2019).

Predators included larvae in the insect order Odonata, and aquatic adults in the orders Coleoptera and Hemiptera (Merritt et al. 2008). We found a negligible number of adult beetles in the family Hydrophilidae, which are herbivores and scavengers, and we excluded this group. Invertebrate predator abundances initially appeared fairly similar among treatments, with a marginally nonsignificant trend in Weeks 3 to 6 toward more in tanks with either kind of plant than water alone (Figure 2, Table 1). In the later period, there was a marginally nonsignificant trend toward more predators in egeria than in hyacinth tanks, with intermediate densities in open water (Table 1). We postulate that predators were abundant in egeria because of preference for some habitat cover, but there may have been fewer predators in hyacinth because of lower prey availability (fewer mosquitoes and competitors) and/or dense leaf cover that would pose a physical or habitat preference barrier to ovipositing predator females. In field studies, egeria has been associated with higher densities of aquatic macroinvertebrates than some other macrophytes, possibly because of the habitat complexity it provides (e.g., Collier et al. 1999, Ferreiro et al. 2011).

Temperature can regulate invertebrate development, most critically larval mosquito growth (Rogers 1967, Silver 2008). Temperature was lower in hyacinth tanks than in other treatments. Water pH varied between treatments, with egeria highest and hyacinth lowest (Table 2, Figure 3); however, pH in all treatments was within larval mosquito tolerances (Rogers 1967, Silver 2008). Percent dissolved

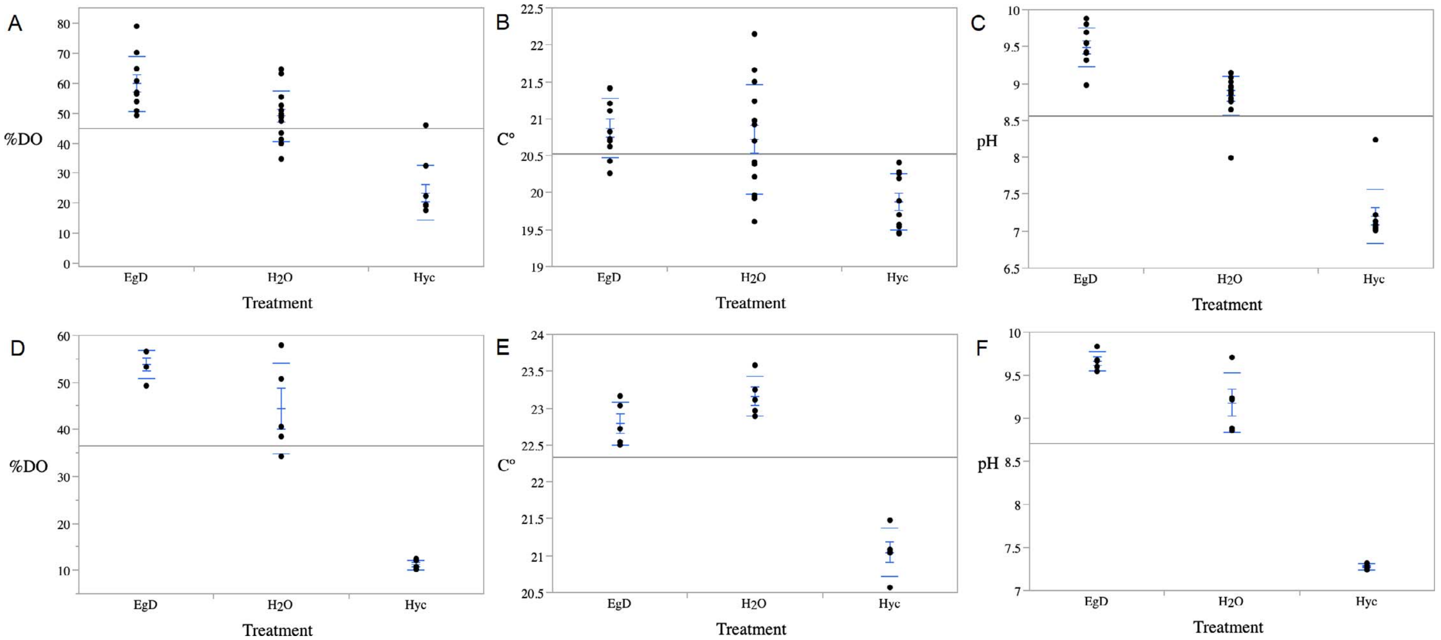

Figure 3. Water quality measures three treatments in early (top row) and later time (bottom row) periods. Treatments were three mesocosm habitats: water, hyacinth, and egeria. Percent dissolved oxygen (%DO): Weeks 3 through 6: A, Weeks 8 through 10: D; temperature (C): Weeks 3 through 6: B, Weeks 8 through 10: E; pH: Weeks 3 through 6: C, Weeks 8 through 10: F. Bars show mean ± SE.

oxygen varied between treatments similarly to pH (Table 2, Figure 3), but larval mosquitoes are atmospheric breathers, so any changes to dissolved oxygen in the water are not expected to have direct effects on mosquitoes. These measures further the hypothesis that the water-quality parameters we measured are not major drivers of differences in mosquito larvae between habitat types. Other invertebrates may have been affected by differences in water-quality measures because these were least abundant in hyacinth tanks, which had comparatively low temperature, dissolved oxygen (DO), and pH (Table 2, Figure 3). For example, oxygen saturation was significantly lower in hyacinth tanks than in other treatments (Table 2, Figure 3). Although DO was mistakenly reported as percent saturation (%DO) rather than parts per million (ppmDO) during much of the experiment, data collected in ppmDO in Weeks 8 and 10 strongly correlated with %DO. Oxygen levels measured ppmDO in water hyacinth were still the lowest (mean = 0.83, SD = 0.14), and similar in tanks with water or egeria (water ppmDO: mean = 3.16, SD = 0.81; egeria ppmDO: mean = 3.64, SD = 0.88; Table 2). DO concentrations below 2 ppm can be lethal to some lentic aquatic insects (Gaufin et al. 1974). This may have contributed to the low abundances of competitors in hyacinth tanks throughout the experiment.

Aquatic plants can play a role in modifying larval mosquito habitats, some contributing to habitat quality and some degrading it (reviewed above and in Turnipseed et al. 2018). Although dense invasive aquatic weeds in the Sacramento–San Joaquin Delta have been assumed by some agencies as being reservoirs for mosquitoes (Ta et al. 2017) and water hyacinth and some other aquatic weeds emit adult attractants (Turnipseed et al. 2018), mosquitoes may in fact not require extensive management in areas with healthy egeria or water hyacinth. Efforts could be better served by controlling mosquitoes in small bodies of open water. A caveat to this conclusion is that our study took place in small containers, where wind and water flow were unlikely to interfere with mosquito development. In larger water bodies, patchy weed beds could serve to protect mosquito larvae, and adjacent open areas could provide enough resources for their development (e.g., Walton et al. 2013). Further research is needed to explore this possibility.

Aquatic vegetation removal can be an effective method of mosquito reduction in some circumstances (Lawler et al. 2007). In many instances, larval mosquito and aquatic weed management overlap in space and time. However, our related work shows that weed control with herbicides can have either positive or negative effects on mosquito populations: oils and surfactants may kill mosquitoes, but weed decay may benefit them (Portilla and Lawler, 2020). Therefore, careful coordination between weed management and mosquito abatement is ideal. This approach is in line with One Health management practices, in which environmental health concerns like the management of invasive taxa dovetails with the protection of public health (Grace 2014, Dente et al. 2019). By understanding how the density and type of aquatic macrophytes in wetland environments affects aquatic macroinvertebrates, we can develop stronger management practices which reduce problematic weeds as well as mosquitoes.

Sources of Materials

1. High Country Plastics, 1502 Aviation Way, Caldwell, ID, USA. 83605
2. Day-old recycling bin, Davis Enterprise, 315 G St., Davis, CA 95616.

3. Ron's Mix, Research Greenhouses, College of Biological Sciences, University of California-Davis, 1 Shields Avenue, Davis, CA 95616.
4. Euro Mum plant pots, Grower's Nursery Supply, Inc., 3695 Clausen Acres Ln SE, Salem, OR, USA 97303.
5. Pack's Water Truck Service, 6349 Rushmore Dr., Sacramento, CA 95842.
6. BioQuip Products, Inc., 2321 Gladwick Street, Rancho Dominguez, CA 90220.
7. Whirl-Pak, Nasco, 901 Janesville Ave., P.O. Box 901, Fort Atkinson, WI 53538-0901.
8. Mosquito Bits "Quick Kill," Summit Chemical Company, 235 S Kresson St, Baltimore, MD 21224.
9. Endurance Metal Cooking Sieve, RSVP International, 4435 Colorado Ave. S, Seattle, WA 98134-2351.
10. Multiparameter System model 9829, Hanna Instruments, 270 George Washington Highway, Smithfield, RI 02917.
11. SM, SMZ10, Nikon Instruments Inc., 1300 Walt Whitman Road, Melville, NY 11747-3064.
12. Microsoft Corporation, One Microsoft Way, Redmond, WA 98052-6399.
13. SAS Institute, 100 SAS Campus Dr, Cary, NC 27513.

ACKNOWLEDGEMENTS

This study was funded by the U.S. Department of Agriculture as part of the Delta Region Area-wide Aquatic Weed Project, Cooperative Agreement 58-5325-4-025 and the William Hazeltine Memorial Student Research Fellowship Award. We thank the following for facilitating the work: J. P. Marie and the U. C. Davis Putah Creek Reserve, the San Joaquin Mosquito and Vector Control District, The Orwood Resort, and Paul Pratt. We also thank our hardworking interns, to whom this paper is dedicated: Taylor Barca, Ivan Beas, Jason Christopher, Chelsea Coppock, Aleah Cornwell, Iris Delgado, Darian Dungey, Michelle Goldina, Joel Hernandez, Henry Hwang, Amrinder Jattana, Hung Kieu, Lydia Kim, Andrew Kobayashi, Rachel Le, Alice Liu, Jessie Liu, Amber Mooney, Abigail Neat, Alexander Robertson, Sana Saeed, Adam Scott, Jim Shen, Kohei Taguchi, Danayit Tsegaye, Priscilla Vasquez-Housely, Nicole Wang, and Joely Zeng. We thank Chris Barker and Eliska Rejmánkova for advice on the project.

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