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Width of planting beds for emergent vegetation influences mosquito production from a constructed wetland in California (USA)

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ABSTRACT

The abundance and distribution of *Culex* spp. mosquitoes, mosquito-eating fish (*Gambusia affinis*), and other macroinvertebrates were assessed within wide (width: 20 m) and narrow (width: 3 m) bands of California bulrush (*Schoenoplectus californicus*) and in the open water adjacent to emergent vegetation in two marshes of an ammonia-dominated wastewater treatment wetland in southern California. Emergence traps and minnow traps were used to collect fauna along transects perpendicular to the path of water flow at three distances (1.5, 5 and 10 m) from the vegetation–open water interface in the wide bands of emergent vegetation, at the center of narrow bands of emergent vegetation and at 1.5 m from the edge of emergent vegetation in the open water. Mosquito production was least from the open water sites and, relative to sites within the wide band of vegetation in each of the two marshes studied, was significantly lower from the narrow bands of emergent vegetation where mosquitofish populations increased comparatively more during the summer and nektonic predatory insects (Notonectidae) were more abundant. Adult mosquito production was greatest at the middle of wide bands of bulrush. Despite an ongoing integrated mosquito management (IMM) program that included routine application of larvicides and adulticides, *Culex* mosquitoes emerged in large numbers (>200 individuals/m^2/day) along transects within the interiors of wide bands of emergent vegetation in the late spring and summer. The width of bands of emergent vegetation in constructed treatment wetlands should be minimized to the greatest extent possible to achieve water quality goals yet to facilitate both ecological and, when necessary, chemical control of mosquitoes.

1. Introduction

Emergent macrophytes fulfill many important roles in treatment wetlands such as creating conditions that enhance filtration and sedimentation of particulates, oxygenation of sediments, providing attachment sites for microbes and other biota, and absorption and transformation of nutrients and other compounds (Brix, 1997; Thullen et al., 2005; Kadlec and Wallace, 2008). While long-term field studies have documented the importance of emergent vegetation for optimizing treatment wetland performance (Sartoris et al., 2000; Smith et al., 2000; Thullen et al., 2002), the spatial configuration (Keefe et al., 2010) and management of emergent macrophytes can significantly influence the performance of constructed treatment wetlands (Thullen et al., 2005).

The planting design and management practices of emergent vegetation also are important components of integrated mosquito management (IMM) for constructed treatment wetlands (Walton, 2002; Knight et al., 2003). Dense vegetation impedes the efficacy of larvivorous fishes such as the mosquitofish (*Gambusia affinis* and *Gambusia holbrooki*) as biological control agents (Gerberich and Laird, 1985; Walton, 2007) and reduces the mortality of mosquito larvae caused by co-occurring insect predators (Walton and Workman, 1998). Expansive zones of emergent macrophytes in ammonia-dominated wetlands greatly reduce the potential habitat for mosquito-eating fishes (Walton et al., 2007). Dense stands of emergent vegetation and mats of decaying macrophytes also impede the penetration to the water surface of most of the current formulations of biorational control agents, such as the spores and mosquitocidal endotoxins of naturally occurring spore-forming soil bacteria (Walton, 2002; Knight et al., 2003).

Emergent vegetation is often planted in contiguous bands oriented perpendicularly to the path of water flow (cross-bands: Kadlec et al., 2010; Keefe et al., 2010). Thullen et al. (2005) recommended the use of raised planting beds (hummocks) oriented perpendicular to the path of water flow and surrounded by deep

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water to manage the growth of emergent vegetation, promote decomposition of senescent macrophytes and enhance water quality performance of surface-flow wastewater-treatment wetlands in which nitrification limited nutrient removal. Isolated raised planting beds studied to date have been comparatively small (surface area: 5.6–37 m^2: Thullen et al., 2002; Keefe et al., 2010). Extending the hummock concept to the cross-bands of emergent vegetation by reducing the width of the raised planting bed between deep water zones to several meters, rather than tens of meters, may help to reduce mosquito production and enhance the wetland treatment processes in constructed wetlands where nitrification needs to be enhanced to meet treatment objectives.

We quantified the abundance of aquatic fauna inhabiting narrow (3 m) and wide (20 m) bands of California bulrush (*Schoenoplectus californicus*), and in adjacent open water zones, at a constructed treatment wetland used to treat ammonia-dominated secondary municipal effluent. In addition to collections of host-seeking mosquitoes, the spatial and temporal trends of mosquito production were measured as part of an IMM program to reduce populations of several pestiferous and pathogen-vectoring mosquito species. We also measured the abundances of co-occurring macroinvertebrates and of potential biological control agents for immature mosquitoes, including the western mosquitofish (*G. affinis*) and predaceous aquatic insects. Ultimately, our objective was to use this information to make recommendations for planting designs for surface-flow constructed treatment wetlands to reduce mosquito production by enhancing natural mortality factors and limit the reliance on chemical insecticides for controlling mosquitoes of public health significance.

2. Site description

The mosquitoes and related fauna were studied in a 9.9-ha surface-flow wetland that received ammonia-dominated secondary-treated municipal wastewater at the Hemet-San Jacinto Regional Wastewater Reclamation Facility (HSJRWRF) in San Jacinto, CA (33°47′52″N, 117°01′19″W; see Sartoris et al., 2000 for site details) during 2005 and 2006. Following a reconfiguration of the site in which the deep-water (operational water depth > 1.5 m) zones were increased from approximately 50% to 70% of the wetland surface area during autumn 2002, the wetland was inundated in May 2003 (Daniels et al., 2010). Two of the shallow marshes (~35 m wide along the path of water flow) at the outflow end of Inlet Marsh 1 and Inlet Marsh 5 (cf. Sartoris et al., 2000) in the second configuration of the site were reconfigured into narrow (width parallel to water flow ~3 m wide) and wide (width parallel to water flow ~20 m) marshes separated by a deep-water zone (~12 m wide; water depth ≥1.5 m: Fig. 1). The length of the cross-band marshes perpendicular to the direction of water flow was approximately 74 m (Inlet Marsh 1) and 62 m (Inlet Marsh 5). The distance from the inlet weir to the open water sampling sites (144 m to sampling sites 28–30: Fig. 1) in Inlet Marsh 5 was approximately 28 m greater than in Inlet Marsh 1; however, no other major physical differences between the marshes were evident.

During periods of stability in the treatment plant operation that provided source water to the demonstration wetland, ammonium–nitrogen concentration typically varied between 16 and 26 mg/L in the influent and the inlet marshes and between 1 and 18 mg/L in the effluent and at the terminus of the outlet marshes (Walton et al., 2007; Nelson and Thullen, 2008; Thullen et al., 2008). Ammonium–nitrogen concentration in the influent water was comparatively low (10.56 mg/L; n = 6, SE = 0.60) during autumn 2005 and winter 2006. Ammonium–nitrogen concentration in the effluent was 8.47 mg/L (n = 6, SE = 1.59) during this period.

3. Methods

Thirty sampling sites were positioned along eight transects in each of the two inlet marshes (Fig. 1). Five transects were established in each wide band of California bulrush (*S. californicus*). A central transect of six trapping sites was located 10 m from the open water on each side of the wide band of emergent vegetation. Transects of three trapping sites were positioned at 5 m and 1.5 m from the open water zones and in the open water at 1.5 m from the vegetation–open water interface on the upstream (inflow) and downstream (outflow) sides of the central transect in the emergent vegetation. A transect of six trapping sites also was run along the center of a narrow band of emergent vegetation. To minimize creating paths along which mosquitofish could move into the interior of the wide band of emergent vegetation, traps on the 5-m and 10-m transects were deployed from paths perpendicular to the direction of water flow (Fig. 1). Traps in the narrow band of emergent vegetation, open water, and the adjacent 1.5-m transect of the wide band of vegetation were deployed using a boat.

Mosquitofish and associated invertebrates were collected using minnow traps (Gee's Minnow Trap, Cuba Specialty Mfg., Co., Fillmore, NY) lined with fiberglass window screen (mesh opening = 1 mm; Walton, 2007) at four time periods: June–July, September, February, and May. Samples were collected on three consecutive weeks (21 June, 28 June and 5 July) during June–July 2005 and during one week in each of the other three time periods. Minnow traps were deployed for 24 h on successive days in each of the two marshes. Each trap was baited with a dog food kibble and contained a float to facilitate respiratory exchange of trapped air-breathing specimens and allow fish access to the comparatively oxygen-rich water at the water surface during periods of extreme hypoxia. Mosquitofish and invertebrates captured by minnow traps were quantified on-site in 11-liter plastic tubs (Rubbermaid Inc., Wooster OH). The standard length (SL), gender and reproductive state (females: non-gravid vs. gravid) of each mosquitofish were noted. Fish were returned to the wetland after processing. Invertebrates were identified to genus or family. When > 100 specimens of a particular invertebrate taxon were collected, individuals were counted in subsamples using a grid marked on the bottom of the plastic tub.

Emerging adult mosquitoes and other invertebrates were collected using 0.25-m^2 floating emergence traps (Walton et al., 1999). Sixty emergence traps (30 per marsh) were deployed concurrently with minnow traps. Emergent vegetation was cut above the water surface to facilitate placement of each emergence trap and to maintain the physical structure below the water surface. A single emergence trap was deployed at each sampling site (Fig. 1) for 4 d during each of the four time periods. Emergence traps were deployed in only July of the first time period. A jar containing an inverted funnel was positioned at the top of each emergence trap. Specimens collected in the jar were returned to the laboratory, frozen, and enumerated at 25×–50× magnification using a stereo dissecting microscope. Mosquitoes were identified to species using Meyer and Durso (1998) and Bohart and Washino (1978). Other invertebrates were identified to family using Merritt and Cummins (1996).

The abundance of female host-seeking mosquitoes was monitored by Riverside County Department of Environmental Health Vector Control (RCDEH) using two CO_2-baited CDC-style suction traps (J.W. Hock Co., Gainesville, FL) located adjacent to the demonstration wetland. The suction traps were deployed overnight on a biweekly basis from April until November. The mosquitoes in the trap collections were identified to species.

Control measures against larval and adult mosquitoes at HSJRWR were carried out by RCDEH from April until October

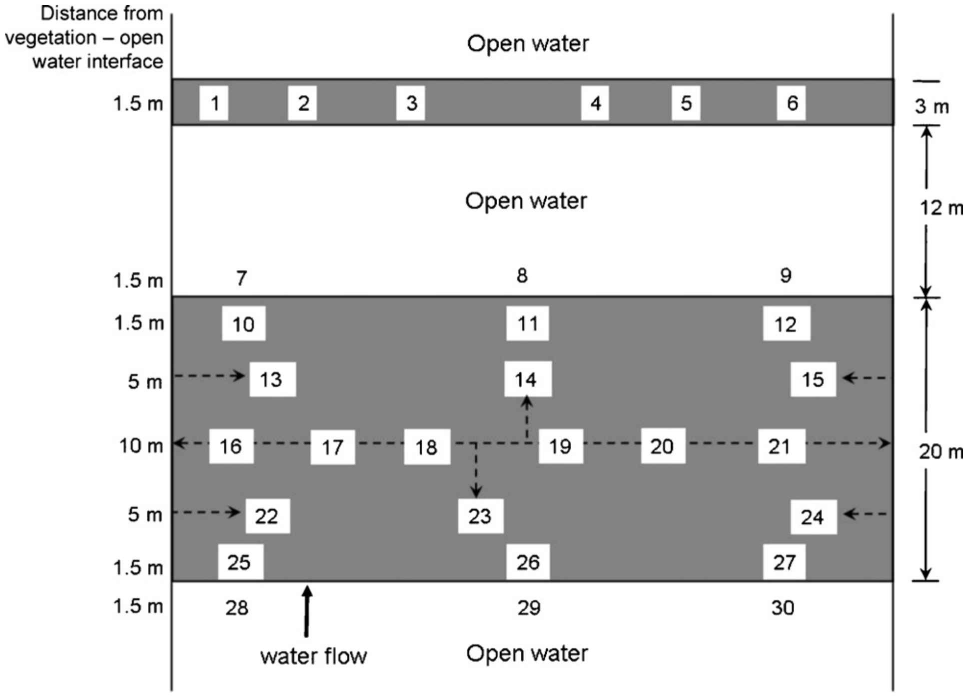

Fig. 1. Schematic drawing of the sampling sites for deployment of minnow and emergence traps in wide (20 m) and narrow (3 m) bands of California bulrush (gray) and open water within two of the marshes of the Hemet/San Jacinto Demonstration Wetland. Dashed lines indicate trails used during trap placement.

2005 and from March until September 2006. Larvicide and adulticide treatments from April 2005 through May 2006 are listed in Table 1. Larvicides [VectoBac® AS (aqueous solution) or G (granules) of *Bacillus thuringiensis* subsp. *israelensis*; VectoLex® CG (corncob granules impregnated with *Bacillus sphaericus*; Valent BioSciences Corp., Libertyville, IL)] and an adulticide (Permanone®, Bayer Environmental Science, Research Triangle Park, NC) were applied weekly or biweekly using truck-mounted and backpack-mounted application technologies.

A multi-parameter water quality sensor array (ICM Water Analyzer, Perstorp Analytical, Wilsonville, OR) was used to measure temperature (°C), dissolved oxygen (DO, mg/L), pH and specific conductance (μS/cm) at representative locations on each of the five transects of Inlet Marsh 1 in July. The sensors were positioned approximately 15 cm below the water surface. Physicochemical variables were measured for 2–3 d at each location and data were recorded every 30 min.

Table 1
Applications of mosquito control agents (adulticide: Permanone®; bacterial larvicides: Vectobac® aqueous suspension (AS) or granules (G), Vectolex® corncob granules (CG)) to the Hemet/San Jacinto Demonstration Wetland during 2005 and through May 2006.

Year	Month	Day	Mosquito control agent
2005			
	April	20	Vectobac G, Vectolex CG
	May	11, 25	Permanone
		4, 11, 18	Vectobac G, Vectolex CG
	June	1, 15, 21, 28	Permanone
		2, 8, 15, 22, 29	Vectobac G, Vectolex CG
	July	6, 7, 11, 13, 18, 25	Permanone
		6, 12, 15, 19, 26	Vectobac G, Vectolex CG
	August	8, 15, 29	Permanone
		2, 9, 16, 30	Vectobac G, Vectolex CG
	September	14, 26	Permanone
		14, 27	Vectobac G, Vectolex CG
2006			
	May	17, 24, 30	Permanone
		17, 30	Vectobac G, Vectolex CG
		19, 23, 25	Vectobac 12 AS

The statistical significance of the effects of transect location, marsh and their interaction on the production of mosquitoes and on the abundance of other insects and mosquitofish across sampling dates were tested using Multivariate Analysis of Variance (MANOVA: SYSTAT v. 9; SPSS, 1998). Hereafter, we use "location" to refer to the group of six replicate sampling sites in open water, at the center of the narrow band of vegetation, or at each of the three distances (1.5, 5, or 10 m) from the open water–vegetation interface in the wide band of vegetation of each marsh. The number of each taxon in each trap collection was $\log_{10}(X+1)$ transformed prior to statistical analysis. Emergence trap data from September 2005 (8 mosquitoes collected in one trap) and February 2006 (0 mosquitoes collected) were not included in statistical models of spatial trends of mosquito production. Adults of non-mosquito insects were rare in February 2006 emergence trap samples (<1 specimen per trap); these data also were removed from statistical tests. ANOVA or a Kruskal–Wallis test (SPSS, 1998) was utilized for single date tests.

The statistical differences of faunal abundance between inflow-side and outflow-side trap replicates of the 1.5-m, 5-m, or open water transects were tested using MANOVA. We did not plan to make these comparisons; the sampling design did not provide sufficient degrees of freedom to test the three-way interaction among location, marsh, and side (inflow vs. outflow) for this subset of traps. However, two-way interactions were never significant ($P > 0.05$) and thus the higher-level interaction terms were excluded from the statistical model.

Multivariate analysis (CANOCO 4.5; ter Braak and Smilauer, 2002) was used to compare invertebrate communities across time and space. Detrended correspondence analysis (DCA) indicated that the gradient length of the dataset was <2 SD. Redundancy analysis (RDA) was used to examine intertaxon associations constrained by habitat heterogeneity over time and space. Sample date, marsh, and transect position were treated as nominal environmental variables. Minnow trap counts from June and July 2005 were

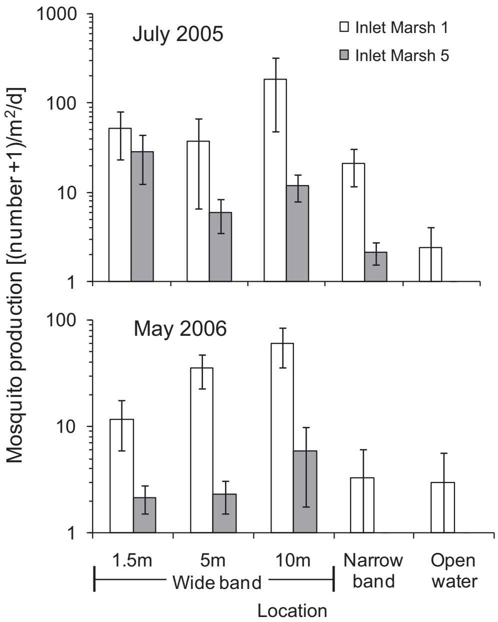

Fig. 2. Adult mosquito production (mean ± SE) from emergent vegetation and open water in two marshes of the Hemet/San Jacinto Demonstration Wetland during July 2005 and May 2006.

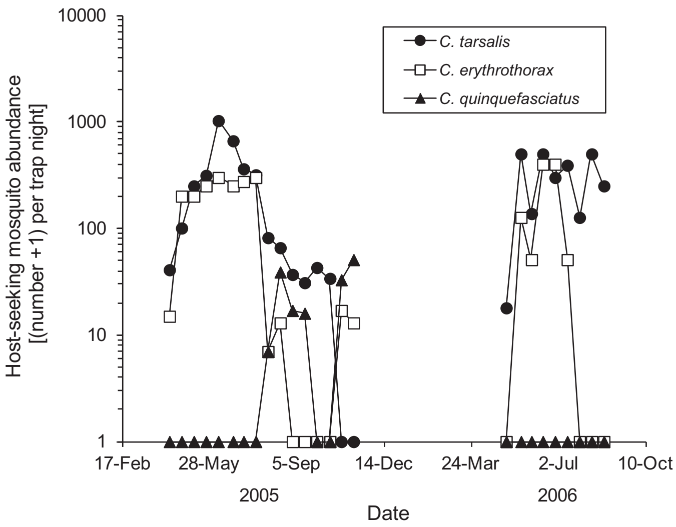

Fig. 3. Host-seeking *Culex* adult mosquitoes collected using CO_2-baited suction traps at the Hemet/San Jacinto Demonstration Wetland 2005–2006.

averaged across sampling periods and corresponded to the 4-day emergence trap collection taken at this time period. Rare taxa with little apparent impact on ordination trends were also removed from the analysis resulting in nine taxonomic categories collected in both trap types in the ordination. All data were $\log_{10}(X+1)$ transformed prior to statistical analysis.

4. Results

4.1. Mosquito production

Mosquito production during the late spring (May 2006) and summer (July 2005) was appreciably greater than during the autumn and winter. Only eight mosquitoes were collected in one emergence trap (at 5 m from the open water-emergent vegetation interface in Inlet Marsh 5) during September 2005 and adult mosquitoes were not collected in February 2006.

During the peak period of annual mosquito abundance in late spring–early summer, mosquito production from emergent vegetation was greater than from open water and, on average, more mosquitoes emerged from the wide bands of vegetation than from the narrow bands of emergent vegetation within each marsh (Fig. 2). Mosquito production differed between the two marshes ($F = 3.790$, $df = 1,49$, $P < 0.057$; Marsh × location: $F = 0.231$, $df = 4,49$, $P > 0.9$). Irrespective of location within each wetland, between 6- and 14-fold more mosquitoes were collected from Inlet Marsh 1 compared to Inlet Marsh 5. Adult mosquito production in both marshes during July differed significantly among locations ($F = 3.818$, $df = 4,49$, $P < 0.009$; open water < 1.5 m and 10 m in wide bands of bulrush; Tukey HSD, $P < 0.05$). Although appreciable variation in mosquito production was observed among traps at a particular location, the mean mosquito production from the center of the wide band of bulrush in Inlet Marsh 1 during July 2005 was nearly 200 individuals/m^2/day (Fig. 2), which was about 100-fold greater than from open water and 10-fold greater than from the same position in Inlet Marsh 5.

Mosquito production was again greatest along the center transect in the wide band of vegetation early in the annual cycle of adult mosquito activity in May 2006 (Fig. 2), but the mean number of emerging mosquitoes was about half that observed during the previous July. Mosquito production differed among locations in both marshes (Kruskal–Wallis test: $H = 15.32$, $df = 4$, $P < 0.004$). Adult mosquitoes were never collected in traps above open water in Inlet Marsh 5 and also were not collected in narrow bands of emergent vegetation in Inlet Marsh 5 during May. Mosquito production differed among the five locations in Inlet Marsh 5 (Kruskal–Wallis test: $H = 10.29$, $df = 4$, $P < 0.036$). After removing the narrow band and open water locations from the ANOVA because mosquitoes were not collected in emergence traps in Inlet Marsh 5, mosquito production differed between the two marshes and among locations within the marshes (Marsh: $F = 30.620$, $df = 1,30$, $P < 0.0005$; Location: $F = 3.354$, $df = 2,30$, $P < 0.048$; Marsh × location: $F = 1.358$, $df = 2,30$, $P > 0.2$). Although 3-fold fewer mosquitoes were collected on average in traps along the 1.5-m and 5-m transects compared to the 10-m transect of Inlet Marsh 5 in May, the variation in mosquito collections among traps was large and the differences were not statistically significant ($F = 0.51$, $df = 5,12$, $P < 0.6$). All emerging mosquitoes were in the genus *Culex* (*Culex tarsalis*, *Culex stigmatosoma*, *Culex erythrothorax*, and *Culex quinquefasciatus*).

Host-seeking mosquitoes in collections from CO_2-baited suction traps were mostly *C. tarsalis* (68% of total) and *C. erythrothorax* (31% of total). The numbers of host-seeking mosquitoes increased during April and were highest (up to 1350 females/trap/night) in June (Fig. 3). Host-seeking mosquitoes decreased to <100 female mosquitoes/trap/night in early August and declined to very low levels by mid-October 2005.

Catches of host-seeking mosquitoes in 2006 did not exceed 1000 individuals/trap/night. Samples of mosquito production from the wetland were collected during a two-week period when host-seeking mosquito populations increased 35-fold during early May.

4.2. Water quality

Dissolved oxygen (DO) concentration in the open water was highest and more variable daily than at the other locations (Fig. 4). The maximum daily DO decreased and the length of the period of severe hypoxia increased directly from the inflow side to the outflow side of the wide band of vegetation. Anoxic conditions were present continuously at locations at the center and on the outflow side of the 20-m band of vegetation in July.

Table 2
Water quality at sampling locations in Inlet Marsh 1 in July.

Location	Variable		
	pH	Conductivity (μS/cm)	Temperature difference (°C)[a]
Open water	7.58 (0.34)	947.0 (44.0)	–
Wide band			
1.5 m inflow side	7.54 (0.23)	966.4 (32.6)	−0.039 (0.340)
5 m inflow side	7.17 (0.05)	1012.0 (10.2)	−0.302 (0.325)
10 m	7.18 (0.08)	1012.1 (13.5)	−0.430 (0.475)
1.5 m outflow side	7.04 (0.03)	1011.0 (12.5)	−0.909 (0.449)
Narrow band	7.22 (0.14)	997.3 (30.7)	−0.367 (0.485)

Standard deviation in parentheses.
[a] Temperature difference is the difference between the water temperature at the location and temperature in the open water on the inflow side of the vegetation bands.

Primary production-driven generation of DO in the open water and emergent vegetation also influenced the other water quality variables at the locations. pH in the open water was highest and more variable than at other locations (Table 2), ranging daily between 7.24 and 8.48. Conductivity within the wide band of bulrush was slightly higher than in the open water and at the periphery of the emergent vegetation. Water temperature declined within the emergent vegetation and was about 1 °C lower in the vegetation on the periphery at the outflow side than in the water column on the inflow side of 20-m bands (Table 2).

4.3. Mosquitofish

Mosquitofish abundance was greatest in September 2005 when counts in minnow traps were an order-of-magnitude higher compared to all other dates (Fig. 5). The marked increase in the size of the fish population was accompanied by a reduction in female mosquitofish body size. Mean female body size declined by 17% from June–July to September (Table 3). The mean body size of male *Gambusia* changed comparatively little during the same period. Although adult mosquitofish collected in February were not markedly larger than individuals collected in the previous September, the body size of males and females in May was larger than in winter. The few overwintering juveniles collected in February were larger than individuals in collections on other dates; however, juveniles were not collected in May. Reproduction during spring and summer resulted in a cohort of smaller fish that replaced the cohort of comparatively large individuals that overwintered in the wetland.

Mosquitofish abundance differed significantly among locations within the two marshes on three of the four sampling dates

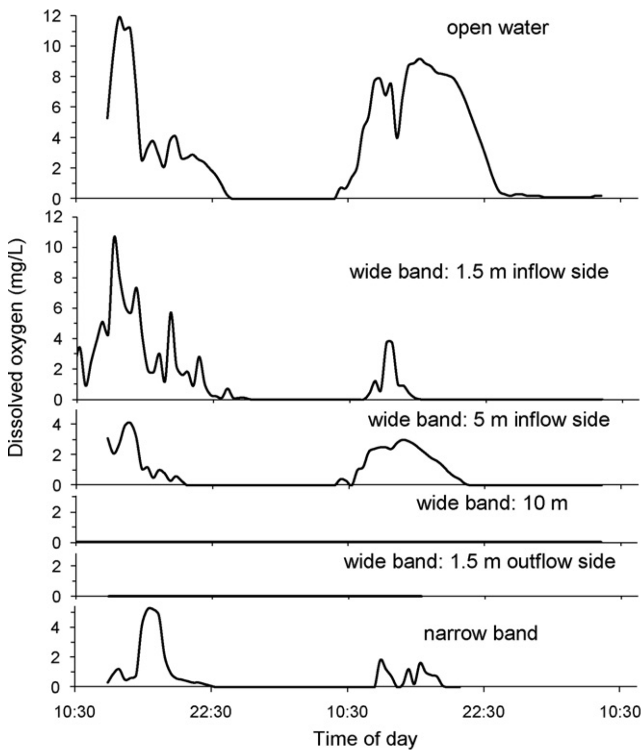

Fig. 4. Dissolved oxygen concentration at six locations in Inlet Marsh 1 in July.

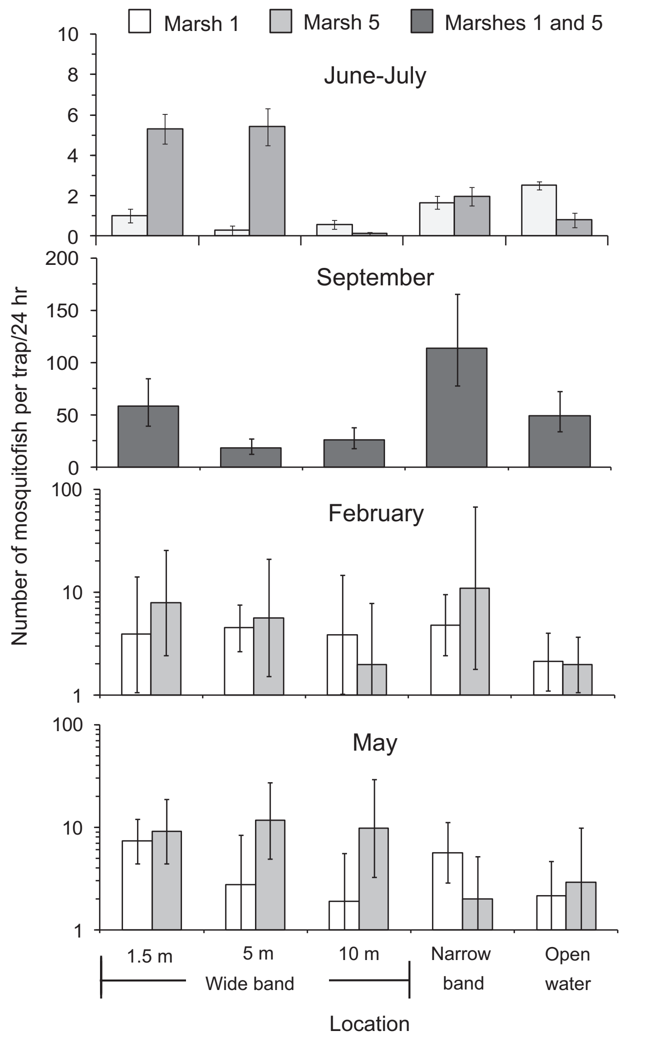

Fig. 5. Mean abundance (±SE: July, September; ±SD: February, May) of *Gambusia* in minnow traps at wetland locations, 2005–2006.

Table 3
Mean standard length (mm) of *Gambusia affinis* collected at the HSJRWRF demonstration wetland 2005–2006.

Date	Group	SL	*n*
June–July 2005	Juveniles	14.7 (3.8)	35
	Males	20.9 (1.9)	586
	Females	32.8 (6.1)	977
September 2005	Juveniles	14.8 (2.7)	334
	Males	21.0 (1.8)	409
	Females	27.3 (6.7)	561
February 2006	Juveniles	16.7 (1.5)	36
	Males	21.1 (1.9)	117
	Females	27.1 (5.6)	341
May 2006	Juveniles	–	0
	Males	23.5 (2.9)	65
	Females	33.7 (4.2)	326

Standard deviation in parentheses.

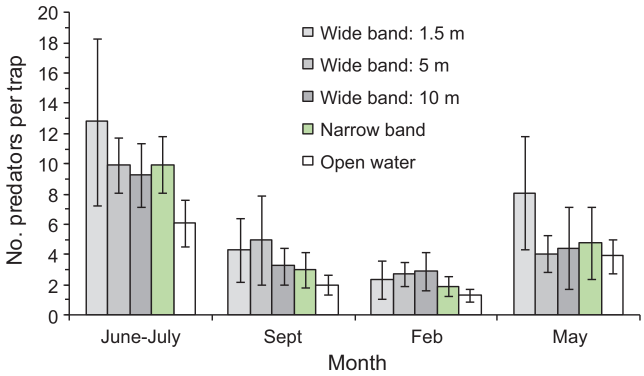

Fig. 6. Mean abundance (±95% CI) of insect predators collected in minnow traps during 2005–2006.

(Table 4); although, the distribution of mosquitofish among locations was not consistent within the two marshes in June–July and May (Marsh × location interaction: $P < 0.05$; Table 4). *Gambusia* abundance tended to be higher in the wide bands of emergent vegetation in Inlet Marsh 5 compared to Inlet Marsh 1 during the two periods of greatest mosquito production. Mosquitofish numbers were, on average, three-fold higher at sites 1.5 m within bulrush compared to those 10 m within bulrush. Mosquitofish were proportionally more common at the center of wide bands of emergent vegetation as the study progressed, increasing from 2% to 24% of the total fish collected on a particular date.

Gambusia affinis was distributed unequally between traps on the inflow- versus the outflow-side of the wide vegetation band within each marsh in June–July and in May (Table 4). Mosquitofish were up to 2.5-fold more abundant at inflow-side locations along the 1.5-m and 5-m transects in wide bands of vegetation. Mosquitofish constituted 35% of the total number of organisms identified from minnow traps during the study.

4.4. Macroinvertebrate community

Invertebrate predator abundance was highest in June–July 2005, declined by 60–80% late in the season and through the winter, and rebounded the following spring (Fig. 6). During summer, the numbers of insect predators collected in minnow traps did not differ significantly among locations in the bulrush but were significantly greater than in open water (Table 4). Predator abundance did not differ appreciably between the two marshes. The most common predacious taxa included giant water bugs (41% of all insects, Hemiptera; Belostomatidae, *Belostoma flumineum*), diving beetles (26%, Coleoptera: Dytiscidae: primarily *Cybister* sp.), dragonfly nymphs (11%, Odonata: Aeschnidae), and backswimmers (6%, Hemiptera: Notonectidae). Belostomatids were the only large insect predator that was prevalent in September and were more abundant on the inflow-side than on the outflow-side of the wide bands of emergent vegetation (Table 4), where immature mosquitoes also were comparatively more abundant. Unlike the three most common predatory insects (belostomatids, dytiscids, and odonates), backswimmers were largely restricted to early summer 2005 (96% of all notonectids collected) and were frequently found in open water, along the edge of wide bands of bulrush and in narrow bands of vegetation.

Predatory insects were the dominant invertebrate guild (77% of total invertebrates) collected in minnow traps except in early summer when detritivorous amphipods were abundant in Inlet Marsh 5. Amphipods (Crustacea: Amphipoda) constituted 93% of all invertebrates captured in early summer and 98% of amphipods were collected from Inlet Marsh 5 during June and July 2005.

Non-mosquito insects comprised 84% of the total number of emerging adults and 98% of these specimens were chironomid midges (Diptera: Chironomidae). Chironomid emergence differed among locations in 2005 (Table 4) and was greatest at 1.5 m inside wide bands of *S. californicus* and least from open water. Midge emergence did not occur in February. Midges were more abundant (>4-fold) in Inlet Marsh 5 than Inlet Marsh 1 in May 2006; however, this trend was not consistent across dates.

Table 4
Effects of marsh, location, and side (inflow versus outflow side of the center transect) on mosquitofish, predatory invertebrates and chironomids.

Source	June–July 2005		September 2005		February 2006		May 2006	
	F-ratio	*P*-value	*F*-ratio	*P*-value	*F*-ratio	*P*-value	*F*-ratio	*P*-value
Mosquitofish								
Marsh	$F_{1,48} = 2.685$	0.108	$F_{1,48} = 0.004$	0.950	$F_{1,48} = 0.708$	0.404	$F_{1,48} = 5.170$	0.027
Location	$F_{4,48} = 2.179$	0.085	$F_{4,48} = 3.717$	0.010	$F_{4,48} = 2.714$	0.040	$F_{4,48} = 3.006$	0.027
Marsh × location	$F_{4,48} = 3.747$	0.010	$F_{4,48} = 1.462$	0.228	$F_{4,48} = 0.636$	0.639	$F_{4,48} = 4.394$	0.004
Side	$F_{1,16} = 6.409$	0.016	$F_{1,16} = 0.826$	0.370	$F_{1,16} = 0.481$	0.493	$F_{1,16} = 5.829$	0.021
Predatory insects								
Marsh	$F_{1,48} = 1.131$	0.289	$F_{1,48} = 0.397$	0.532	$F_{1,48} = 0.014$	0.908	$F_{1,48} = 0.000$	0.989
Location	$F_{4,48} = 4.428$	0.002	$F_{4,48} = 1.603$	0.188	$F_{4,48} = 2.474$	0.056	$F_{4,48} = 1.875$	0.129
Marsh × location	$F_{4,48} = 1.046$	0.385	$F_{4,48} = 0.512$	0.727	$F_{4,48} = 0.126$	0.972	$F_{4,48} = 0.715$	0.585
Side	$F_{1,16} = 0.000$	0.999	$F_{1,16} = 13.491$	0.001	$F_{1,16} = 0.127$	0.724	$F_{1,16} = 0.009$	0.925
Chironomids								
Marsh	$F_{1,48} = 2.126$	0.151	$F_{1,48} = 0.740$	0.394	–		$F_{1,48} = 26.218$	0.047
Location	$F_{4,48} = 2.585$	0.048	$F_{4,48} = 2.610$	0.047	–		$F_{4,48} = 1.986$	0.111
Marsh × location	$F_{4,48} = 0.872$	0.488	$F_{4,48} = 1.631$	0.181	–		$F_{4,48} = 1.702$	0.165
Side	$F_{1,16} = 0.304$	0.585	$F_{1,16} = 16.750$	0.001	–		$F_{1,16} = 1.872$	0.180

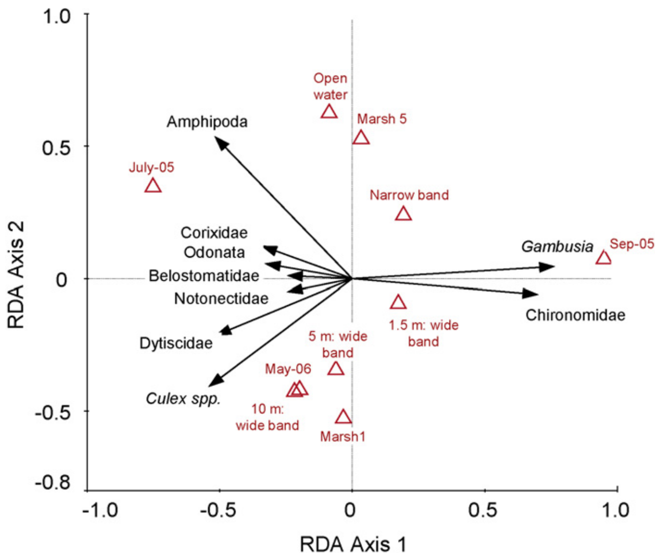

Fig. 7. Redundancy analysis (RDA) of spatial and temporal trends in minnow and emergence trap collections.

4.5. General patterns in the animal community

After forward selection of the environmental variables, the RDA model included three sample dates, marsh, and three of the locations (open water, 10 m and 5 m). The first two axes of the model explained 87.3% of the variance in the fitted species data for nine taxa and 43% of the total variation in common taxonomic groups from emergence and minnow traps. The species-environment correlations of the first two axes were 0.847 and 0.626. Axis 1 was largely a function of seasonal changes among sampling periods and axis 2 was primarily related to spatial variability in the wetland (Fig. 7).

Mosquitofish and chironomid midge abundances peaked during September and, across the study, were higher within emergent vegetation near open water (i.e., 1.5 m in wide band and narrow band) as compared to other locations (Fig. 7). In contrast to *Gambusia* and midges, mosquitoes and co-occurring macroinvertebrates were common during the late spring and early summer. The comparatively higher abundance of *Culex* mosquitoes in Inlet Marsh 1 and differences of mosquito production between wide versus narrow bands of emergent vegetation are evident in the relative positions of the centroids for spatial locations along the axis of *Culex* spp. in the ordination (Fig. 7). Across the entire study, mosquito production was positively associated with wide bands of emergent vegetation and differed across the locations (wide band (10 m > 5 m > 1.5 m) > narrow band > open water). Mosquito production was independent of the abundance of amphipods, positively associated with the abundance of large adult predaceous water beetles (Dytiscidae) and negatively associated with the abundance of *G. affinis*.

5. Discussion

The structure of the aquatic community differed spatially in a constructed wetland processing ammonia-dominated secondary-treated municipal wastewater and the production of mosquitoes also differed spatially in the emergent vegetation in the wetland. Mosquito production was least from the open water sites. Despite an ongoing IMM program that included larvivorous fish and routine application of mosquito larvicides and adulticides, mosquito production from the center of 20-m wide bands of California bulrush oriented perpendicular to the path of water flow was significantly higher than from narrow (3-m width) bands of California bulrush.

Several factors contributed to the high mosquito production at the center of wide bands of emergent vegetation. First, the abundance of mosquito-eating fish at the center of wide bands of *S. californicus* was comparatively lower than at the periphery of wide bands of emergent macrophytes, in narrow bands of bulrush, and in open water. This spatial distribution of *Gambusia* was evident in trap collections in Inlet Marsh 5 on both dates in 2005 and in Inlet Marsh1 on all dates except February when mosquitofish populations were smallest annually. The positions of the centroids for trapping locations relative to the axis for *Gambusia* in the ordination (Fig. 7) indicate that during this study mosquitofish abundance was generally greatest and equivalent in the narrow vegetation band and at the periphery of the wide band of bulrush, and was least at 10 m from the open water-vegetation interface in the middle of wide bands of *S. californicus*.

A reduced abundance of mosquitofish in the wider bulrush bands could have been related to physical restriction of fish movements caused by dense bulrush stands and persistent low dissolved oxygen concentrations within the wide bands of emergent vegetation. In previous studies (Thullen et al., 2002; Popko, 2005), bulrush culm densities in experimental wetlands at the HSJR-WRF generally averaged between 200 and 400 culms/m^2, with patches > 800 culms/m^2. Emergent vegetation provides refuge from important mortality factors (e.g., predation, cannibalism, abiotic stressors, etc.) and enhances resources for growth and reproduction of *Gambusia* (Collins and Resh, 1989; Swanson et al., 1996; Walton, 2007). Non-predation mortality of sentinel mosquitofish in cages in open water was 50% higher than for fish residing in cages encircled by bulrush near the vegetation-open water interface in an ammonia-dominated constructed treatment wetland in the Coachella Valley, California (Popko et al., 2009). The maintenance of circumneutral pH within stands of emergent vegetation reduced the potential negative effects of conversion of ammonium to ammonia that occurred during the diel changes of pH associated with primary production in open water. However, high plant densities limit the movement of mosquitofish (Collins and Resh, 1989; Swanson et al., 1996). Since high fish density is an important prerequisite for significant mosquito reduction (Swanson et al., 1996), smaller *Gambusia* populations in densely vegetated environments are less likely to be successful biological control agents.

Peck and Walton (2008) found that both mosquitofish and predatory insects had significant effects on larval mosquito abundance at the interface of emergent vegetation and open water, irrespective of position along the nutrient gradient in this wetland. Nevertheless, adult production of some mosquito species was directly related the resource gradient across the treatment wetland. Relative to sites within the wide band of California bulrush in each of the two marshes studied, the number of emerging adult mosquitoes was significantly lower in emergent vegetation where mosquitofish populations increased comparatively more during the summer and nektonic predatory insects (Notonectidae) were present.

Greenway et al. (2003) and Dale et al. (2007) suggested that, compared to monotypic stands of emergent vegetation (e.g., *Typha*), macrophyte diversity enhanced the diversity of mosquito predators. Macrophyte species differ in their propensity to produce mosquitoes and concurrently fulfill other functions within wetlands (Collins and Resh, 1989; Knight et al., 2003). Greenway et al. (2003) concluded that top-down effects from mosquito predators influences mosquito production more than bottom-up effects of nutrient enrichment. Nutrient gradients did not influence larval mosquito abundance in four treatment wetlands studied by Greenway et al. (2003). They recommended that treatment wetlands should be designed and managed to maximize macroinvertebrate predators because predation by aquatic invertebrates controls larval mosquito numbers and prevents the development of pupae.

Seasonal water management in the wetland contributed to the movement of mosquitofish into the center of the wide bands of bulrush across this study. Relative to water depths in the summer and autumn 2005, water level in the wetland was raised by approximately 50–60 cm in the winter and remained high through May 2006. As inundated decaying plant matter sunk during the winter and early spring, a zone of open water developed in the direction of water flow along the south side of the Inlet Marsh 5 during 2006. This open water zone allowed mosquitofish to penetrate into the wide band of emergent vegetation and move along the paths used to set and retrieve traps. The marked reduction of the mosquitofish population between September and February indicates that overwintering survival of *G. affinis* is low (< 10%). The variability of mosquitofish collections in February and the similarity of trap collections of *Gambusia* across locations of the wide vegetation band in Inlet Marsh 5 in May (Fig. 5) are indicative of the small overwintering populations and the movement of mosquitofish into the emergent vegetation. Based on the size distribution of the mosquitofish population and the continued low numbers of mosquitofish in trap collections from February until May, reproduction is very low during the period immediately preceding the vernal maximum of mosquito activity in June and early July.

Raising wetland water levels seasonally enhances the sinking of dead plant matter and aids the movement of larvivorous fish into regions of the wetland where fish abundance was low previously. Fluctuating water levels have been shown to increase decomposition rates of plant matter (Neckles and Neill, 1994; Lockaby et al., 1996; Spieles and Mora, 2007); although, sinking of dead plant matter without repeated drying and wetting slows decomposition rates (Thullen et al., 2008). Collins and Resh (1989) noted that trails in dense vegetation are vital to dispersal of fish in natural wetlands and found that fish density declined and mosquito abundance increased at distances greater than 25 cm from trail edges. Trail effects may have been lessened somewhat in our study because traps were placed ~25–50 cm away from the open water in the trails shown in Figure 1.

Chironomid midges and mosquitofish responded similarly to spatial differences in the demonstration wetland across this study. The abundances of both organisms across this study were associated positively (Fig. 7). A previous study (Peck and Walton, 2008) using enclosures and fish exclusion cages in this wetland also found that *Gambusia* does not significantly affect chironomid abundance.

Low dissolved oxygen concentrations in extensive stands of emergent vegetation influence macroinvertebrate community structure (Nelson and Thullen, 2008) and limit the distribution of fish, especially for species that are not capable of utilizing oxygen at water surface (Walton et al., 1996, 2007). Dale et al. (2002, 2007) found that high numbers of mosquito larvae were associated with low DO concentration. Nelson and Thullen (2008) suggested that constructed wetland designs that encourage production and maintenance of high DO concentration will encourage microbial and invertebrate processing of dead plant matter. Dissolved oxygen concentration in open water tends to be higher than in emergent vegetation (Swanson et al., 1996; Sartoris et al., 2000); however, hypoxic conditions were present after dark even in the open water in this wetland. DO levels in bulrush closer to open water on the inflow side of wide bands of vegetation were higher during daylight than in bulrush at the center of stands of vegetation. DO concentration was extremely low on the outflow side of wide bands of bulrush. The availability of oxygen in the water column not surprisingly influenced the distribution of mosquito-eating fish and predatory insects such as immature odonates that respire across the cuticle and via tracheal gills. The majority of the insect predators (i.e., predatory beetles, water bugs, and backswimmers) utilize atmospheric oxygen for respiration. Low dissolved oxygen concentration will influence the rate of oxygen depletion within air stores (Matthews and Seymour, 2006) but is not expected to limit the distribution of air-breathing insects.

A second factor contributing to high levels of mosquito production in the center of wide bands of emergent vegetation was the spatial distribution of important insect predators of mosquitoes. Insect predators such as giant water bugs (*Belostoma*) and large adult predaceous water beetles (*Cybister*) probably rarely consume immature mosquitoes. However, nektonic backswimmers (*Notonecta*) are important predators of immature mosquitoes (Chesson, 1984; Walton and Workman, 1998). Predatory backswimmers were collected mostly in June and July, were generally restricted to open water and the periphery of emergent vegetation and were rarely collected at 5 m and 10 m into wide bands of bulrush.

A third factor contributing to the high mosquito production in the centers of wide bands of emergent vegetation was an inability to distribute larvicidal agents effectively into this zone. Truck-mounted and backpack-mounted application technologies used to apply comparatively environmentally friendly bacterial larvicides cannot effectively penetrate dense vegetation in the center of 20-m wide bands emergent vegetation. The effective distance of application for granular formulations of bacterial larvicides by the equipment used during this study is only 4.5–6 m (15–20 feet). Even though the weekly or biweekly applications of larvicides and ultra-low volume applications of chemical adulticides reduced the annual maximum of host-seeking populations by more than an order of magnitude relative to the large adult mosquito populations observed before an IMM program was implemented at the demonstration wetland [cf. <1350 individuals/trap/night (Fig. 3) vs. >33,000 individuals/trap/night (Walton et al., 1998)], mean mosquito production at the center of the wide band in Inlet Marsh 1 was still nearly 200 individuals/m^2/day in July. Six- to 14-fold more mosquitoes emerged from the larger stand of bulrush in Inlet Marsh 1 as compared to Inlet Marsh 5. Walton (2009) found that on average only about 76% of emerging mosquitoes are collected by emergence traps and, because recently emerged mosquitoes rest within the emergence trap before moving into the collection jar, a 4-day trapping period collects about 50% of emergent mosquitoes when production is continuous during the trapping period. Consequently, production of *Culex* mosquitoes may have ranged between 250 and 500 mosquitoes/m^2/day in the center of the larger of the two wide bands of bulrush. Regardless, the IMM program not only reduced the size of the host-seeking mosquito population in early summer during a period important for arbovirus amplification, the numbers of host-seeking mosquitoes were also reduced markedly in the late summer and autumn when arbovirus infections often occur in humans (CH2M HILL, 1999; Barker et al., 2010). West Nile virus was detected in mosquito pools collected during 2005 (B. Hess, unpublished data).

Mosquito production in mid-September may have been underestimated because adulticides were applied at the midpoint of the collection period. The adulticide might have killed recently emerged mosquitoes which had not yet entered collection jars affixed to the apex of the emergence traps. The numbers of host-seeking adults collected by CO_2-baited suction traps remained at comparable but low levels (between 30 and 45 *C. tarsalis* females/trap/night) through 13 October, indicating that mosquito production was ongoing. Emergence trapping on other dates did not overlap with adulticide applications.

California bulrush planting beds <10 m in width, in conjunction with an IMM program, reduced mosquito production from this constructed treatment wetland. In addition to enhancing ecological processes that cause mortality of immature mosquitoes and reduce mosquito production, restricting the width of planting beds to <10 m should reduce the cost and enhance the efficacy of mosquito control by lessening the area of vegetation treated with mosquito control agents and eliminating regions of emergent vegetation that are inaccessible using ground-based application technologies. Expansive coverage (75–80%: Daniels et al., 2010) of the wetland surface by emergent vegetation in the prior configurations of the wetland required the use of aircraft to apply mosquito control agents (Walton et al., 1998). The use of aircraft approximately doubles the cost of mosquito abatement (Walton, 2002).

Even though mosquito production from narrow (3 m wide) bands of emergent vegetation was either greatly reduced or eliminated seasonally, the comparatively wider bands of vegetation offer benefits for nitrogen removal by providing internal storage and a zone of persistently low DO where denitrification is enhanced. Smith et al. (2000) found that denitrification rates in the sediments of vegetation zones were about twice those in the sediments under open water and that internal storage accounted for about 60% of the nitrogen removal one year after first reconfiguration of the wetland. In contrast to the center and outflow side of the 20-m bands of vegetation, DO was present in the center of narrow 3-m bands of bulrush for a portion of the day. Although the DO was present for a portion of the diel period at 5 m into the wide band of *S. californicus*, prior work indicated that severe hypoxia was persistent at 5 m into the emergent vegetation of the inlet marshes (Walton et al., 2007). The higher DO at the 5-m location in the current study was caused by the sensor array being positioned near a natural opening in the vegetation where photosynthesis-derived DO production occurred.

Previous authors suggested that maintaining narrow vegetated areas may be difficult and expensive in shallow large-scale wetlands (Collins and Resh, 1989; Jiannino and Walton, 2004); but, restricting emergent vegetation to raised planting beds interspersed with deep water zones that do not support emergent vegetation will reduce the frequency of vegetation harvesting and improve water quality performance of constructed wetlands receiving ammonia-dominated effluent (Thullen et al., 2002, 2005). The spacing between the raised planting beds should be large enough to maintain open water if emergent vegetation cannot maintain upright stands and collapses onto the water surface. Positioning narrow cross-bands of emergent vegetation near the inflow of surface-flow wetlands may afford the same potential benefits for enhanced levels of nitrification provided by isolated hummocks (Thullen et al., 2005; Keefe et al., 2010), but reduce the potential for preferential water flow around islands of vegetation. Incorporation of wider bands of emergent vegetation near the outflow is expected to enhance nitrogen removal and to reduce particulates contributing to total suspended solids and biological oxygen demand in the water column (Thullen et al., 2005). However, depending on loading rates and treatment wetland processes, the persistent anoxia observed in the emergent vegetation of the inlet marshes may not be present at ≥5 m into emergent vegetation of the outlet marshes (Walton et al., 2007). Continued development of habitat design and management strategies, including IMM, and a greater understanding of their roles in shaping the structure and function of the biotic community are needed to enhance the ecological interactions that minimize the production of pathogen-transmitting mosquitoes from this promising technology for wastewater treatment and reclamation.

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