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Characterizing macroinvertebrate community composition and abundance in freshwater tidal wetlands of the Sacramento-San Joaquin Delta

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Abstract

Restored tidal wetlands may provide important food web support for at-risk fish species in the Sacramento-San Joaquin Delta (Delta) of California, including Delta Smelt (*Hypomesus transpacificus*) and Chinook Salmon (*Oncorhynchus tshawytscha*). Since many tidal wetland restoration projects are planned or have recently been constructed in the Delta, understanding the diversity and variability of wetland invertebrates that are fish prey items is of increasing importance. During this study, two different invertebrate sampling techniques were tested (leaf packs and sweep nets) in four habitat types within three different wetland areas to evaluate which sampling technique provided the most reliable metric of invertebrate abundance and community composition. Sweep nets provided a better measure of fish food availability than leaf packs and were better able to differentiate between habitat types. Generalized linear models showed submerged and floating vegetation had higher abundance and taxa richness than channel habitats or emergent vegetation. Permutational multivariate analysis of variance showed significantly different communities of invertebrates in different habitat types and in different wetlands, and point-biserial correlation coefficients found a greater number of mobile taxa associated with sweep nets. There were more taxa associated with vegetated habitats than channel habitats, and one area had more taxa associated with it than the other two areas. These results suggest that restoration sites that contain multiple habitat types may enhance fish invertebrate prey diversity and resilience. However, the effect of habitat diversity must be monitored as restoration sites develop to assess actual benefits to at-risk fish species.

Introduction

Tidal wetlands provide an important source of productivity to many estuaries worldwide, subsidizing the surrounding open-water areas with vascular plant detritus, phytoplankton,

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zooplankton, and nekton biomass [1–5]. Productive freshwater tidal wetlands dominated the landscape of California's Sacramento-San Joaquin Delta (Delta) prior to the Gold Rush, but, by 1930, the vast majority of wetlands were reclaimed, primarily for agriculture [6] (see Fig 1A). While there is currently no quantitative estimate of the impact of wetland loss on aquatic primary productivity, production most likely declined drastically post-reclamation [7].

Restoration of tidal wetland habitat in the Delta may increase overall primary and secondary production, and thus multiple regulatory mandates now include tidal wetland restoration as part of the recovery effort for several threatened and endangered native fish species, including Chinook Salmon (*Oncorhynchus tshawytscha*) and Delta Smelt (*Hypomesus transpacificus*) [10–13]. Restoration sites of varying size and type are being planned in various locations throughout the Delta and neighboring Suisun Marsh. However, there is a lack of understanding of how to quantify invertebrate abundance within wetlands, and limited knowledge on how invertebrate communities vary within and between wetlands.

The current Delta ecosystem is dominated by deep channels, steep, rip-rapped levee banks, and tidal lakes [6]. The aim of wetland restoration is to create a more complex mosaic of habitat types that are believed to be beneficial as fish habitat and for invertebrate production. This mosaic includes shallow, subtidal habitat that provides high phytoplankton production [14] and directly increases pelagic secondary production [15]. Intertidal zones dominated by emergent aquatic vegetation (EAV) also provide a subsidy of detrital carbon and a substrate for epiphytic algae and invertebrates [3, 16, 17]. Wetlands contain complex tidal channel networks that allow fish to access the food produced in the intertidal zone and provide refuge from predation [18–21]. These diverse habitat types may support unique invertebrate communities, which must be quantified in order to show the effectiveness of wetland restoration.

Some habitat types are not directly targeted by wetland restoration, but often occur in restored habitats and may also provide valuable fish food sources. Habitats dominated by invasive submerged aquatic vegetation (SAV), such as Brazilian waterweed (*Egeria densa*), and floating aquatic vegetation (FAV), such as water hyacinth (*Eichhornia crassipes*), have been implicated as negative for native fish in the Delta due to high occupancy by invasive predatory fish [22, 23], and adverse effects on water quality [24, 25]. However, invasive vegetation may also provide substrate for large numbers of epiphytic invertebrates [26–28]. Brazilian waterweed and water hyacinth are particularly common in shallow-water habitats, have been expanding rapidly, and do not respond well to control efforts [29], so while restoration plans often try to limit the establishment of SAV and FAV, invasive vegetation will be inevitable at some locations.

Despite the need to assess restoration effectiveness, there is no recognized standard for sampling epibenthic and epiphytic invertebrates in wetlands. There is broad recognition that multi-habitat sampling is needed to assess variation in invertebrate communities in stream systems [30], so we wanted to find a single sampling method that works in multiple habitats. Many previous studies have been conducted to determine the most effective collection methods for invertebrates in standing water, but there is currently no one method that is broadly agreed upon in the United States [31]. Some methods, such as drop-frames, may provide high-quality data, but can be time and cost prohibitive [32]. Other methods, such as Hester-Dendy disk sets, have provided good data in some systems [31] but are highly dependent on abiotic variables, and early trials in the Delta yielded very low catch [33]. Invertebrate sampling methods that have been employed in other wetlands often prioritize diversity and presence of sensitive species (as an index of biotic integrity) rather than biomass or abundance (e.g. [34–36]). Furthermore, wetland conditions, such as tidal influence, topographic complexity, and vegetation structure, vary between bioregions. Because of this, a method that has been proven effective in the sawgrass prairies of the Everglades (for example) may not work in the tule

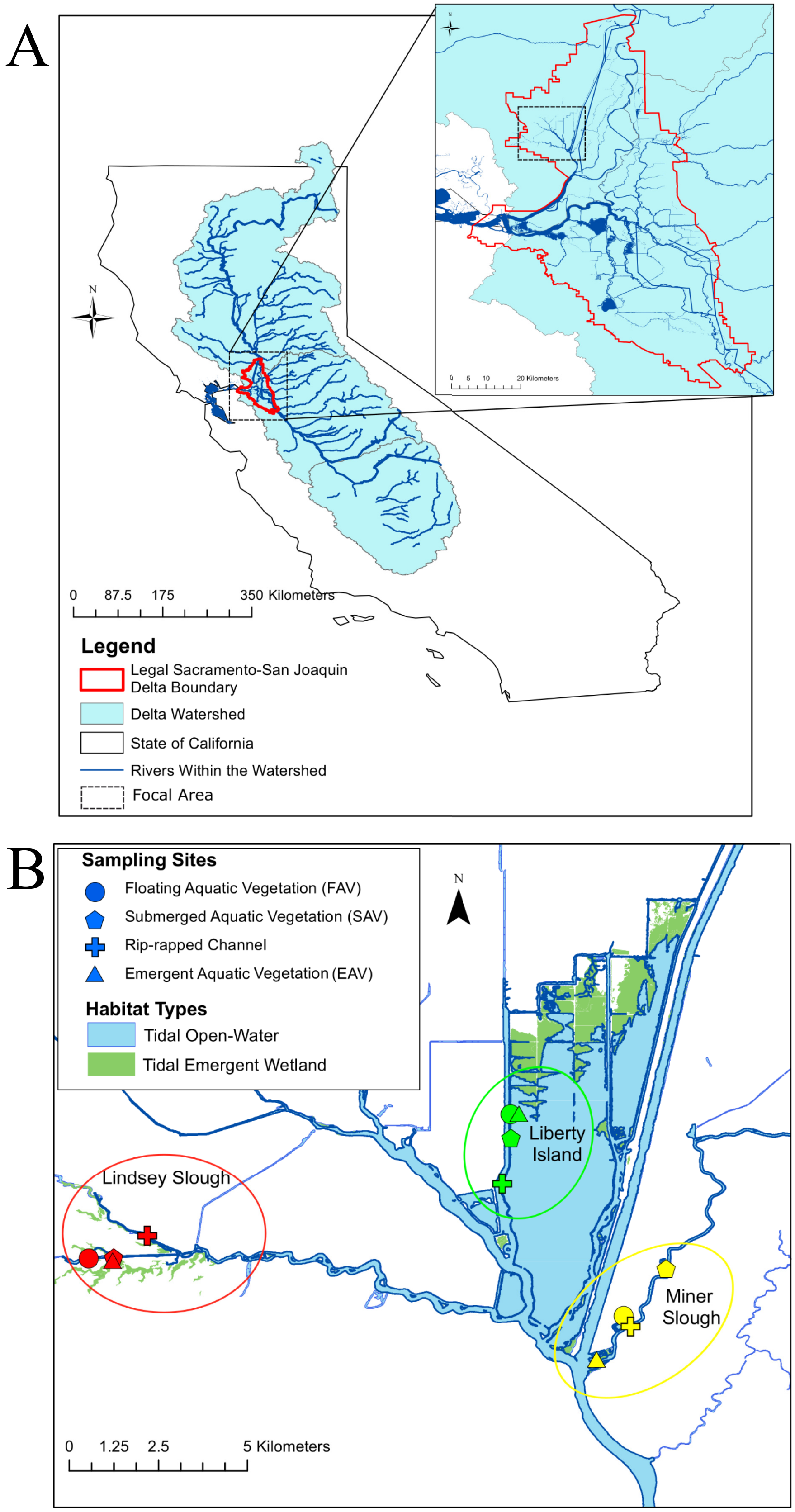
A
0 5 10 20 Kilometers
0 87.5 175 350 Kilometers
N
Legend
Legal Sacramento-San Joaquin Delta Boundary
Delta Watershed
State of California
Rivers Within the Watershed
Focal Area
B
Sampling Sites
Floating Aquatic Vegetation (FAV)
Submerged Aquatic Vegetation (SAV)
Rip-rapped Channel
Emergent Aquatic Vegetation (EAV)
Habitat Types
Tidal Open-Water
Tidal Emergent Wetland
N
Liberty Island
Lindsey Slough
Miner Slough
0 1.25 2.5 5 Kilometers

Fig 1. A) Map of California (USA) with the San Francisco Bay-Delta watershed. The inset is a finer-scale map of the Delta, with the focal region in the Cache Slough Complex outlined with a dashed box. **B)** The Cache Slough complex, with sampling areas circled. Each area contained four sampling stations, each with a different habitat type: SAV, FAV, EAV, or Channel. Maps are the product of the author, and use data from the National Watershed Boundary Dataset [8] and CDFW's Vegetation Classification and Mapping Program [9].

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(*Schoenoplectus* spp.) marshes of the Delta [37]. To determine whether wetland restoration provides increased food for at-risk fishes, studies should evaluate differences in invertebrate density and biomass over time and between habitats. Wetlands are a mosaic of different habitat types, so methods to measure invertebrate biomass must work consistently across all habitats.

We hypothesized that a passive colonization substrate sampler, which could be deployed in the same way in multiple habitats, would provide a more controlled measure of invertebrate abundance than active methods (such as nets or benthic grabs). However, active methods generally sample a higher volume than passive methods, potentially increasing total catch. We were unsure whether the potential reduction in variability would be worth the increased effort required by the multiple trips to the sampling locations necessary for colonization substrates. Therefore, after an extensive literature review, we conducted preliminary trials of multiple passive methods (Hester-Dendy disk sets, mesh scrubbers, and leaf packs), and compared them against multiple active methods (sweep nets, Marklund samplers, throw traps) to determine which were feasible for a study with higher replication (full results available in [33]). Hester-Dendy disk sets and mesh scrubbers had very low catch, resulting in low power for comparing community composition. Throw traps, which have been very successful in other wetlands [32, 37], did not work well in the tall, thick tule marshes of the Delta. Marklund samplers were difficult to use effectively and had few comparable studies [38]. Of these methods, sweep nets were the most effective active method and leaf packs were the most effective passive method.

In this study, we followed up on our previous trials and evaluated leaf packs, colonization substrates made of standardized bundles of the dominant vegetation left in the wetland for several weeks (as used in [39]), and sweep nets (d-frame nets swept through the water several times by hand, as used in [37]) to see which was most effective in describing the relative abundance of invertebrates. Leaf packs are commonly used for stream systems but are also used in wetland and estuarine systems where there is extensive emergent vegetation [39–41]. Sweep nets often capture higher invertebrate species diversity than colonization substrates, though with higher variability in biomass [37]. This study targeted epiphytic and epibenthic invertebrates, as well as larger zooplankton; taxa include amphipods, isopods, aquatic insects, and larger cladocerans and copepods.

We had three major research questions in this study:

1. How do leaf packs compare to sweep nets in collecting a sample of the invertebrate community?
    a. Which sampling method has higher power to differentiate between habitat types?
    b. Which sampling method has higher power to differentiate between wetlands in neighboring areas?
2. How do invertebrate communities change across wetland habitat types?
3. How do invertebrate communities change between wetlands in neighboring areas?

We hypothesized that leaf-packs would be easier to standardize across habitat types, and thus provide a lower-variance, higher-power method to differentiate between habitat types and wetland sites. We expected relatively large differences in community composition between habitat types, but small differences between wetlands in neighboring areas.

Methods

Sample location and timing

We conducted two intensive bouts of sampling, one on March 16–17, 2016, and one on May 2–3, 2016. Because salmon and smelt are both anadromous and semi-anadromous, respectively, they are not present in the freshwater wetlands year-round. Spring (February-May) is the period of upstream migration of Delta Smelt and the peak period for residence of juvenile salmonids [42–44]. This is not the period of highest amphipod and insect abundance [2, 28], but the salmon and smelt that consume these are present at their highest densities, and are therefore most able to take advantage of the available invertebrates.

All samples were collected in the Cache Slough Complex, a region in the north-east Delta with high freshwater tidal wetland restoration potential because of high native fish density and appropriate intertidal elevations (Fig 1B, Table 1)[44, 45]. We chose three areas within the Cache Slough Complex to provide a range of wetland habitats: 1) Liberty Island, 2) the downstream end of Miner Slough and its adjacent marshes, and 3) the Lindsey Slough Restoration site. Liberty Island, an island formerly diked for farming, was flooded by an accidental levee breach in 1997 and contains one of the largest emergent tidal marshes in the present-day Delta. Miner Slough is a distributary of the Sacramento River that flows past Prospect Island, a future tidal wetland restoration site [46]. Lastly, Lindsey Slough Restoration Site is a dead-end slough (slow moving channel) with a formerly diked wetland that was restored to tidal action in the fall of 2014. All three sites were in public waterways or land owned by the California Department of Fish and Wildlife (CDFW).

Description of habitat types

In each area, we targeted four habitat types typical of tidal wetlands. Emergent aquatic vegetation (EAV) sampling stations were in dense stands of native tules (*Schoenoplectus* spp). Submerged aquatic vegetation (SAV) sampling took place in dense stands of invasive Brazilian water weed (*Egeria densa)*. Floating aquatic vegetation (FAV) sampling was conducted in

Table 1. Sampling stations and habitat types, with average environmental parameters when samples were collected. DO = dissolved oxygen in milligrams per liter, Temp = surface temperature in degrees Celsius, SC = specific conductance in micro-Siemens per centimeter, Turb. = Turbidity in nephelometric turbidity units, and Depth of water in meters. Latitude and Longitude are in WGS 1984.

Area	Habitat Type	Latitude	Longitude	DO (mg/L)	Temp (°C)	SC (μS/cm)	Turb. (NTU)	Depth (m)
Liberty Island	Channel	38.27850	-121.6940	9.6	16.4	306	42.5	0.74
Liberty Island	EAV	38.29617	-121.6899	11.5	17.7	351	27.7	0.80
Liberty Island	FAV	38.29607	-121.6919	11.3	17.6	341	21.8	1.08
Liberty Island	SAV	38.29003	-121.6918	11.2	18.6	347	29.9	1.22
Lindsey Slough	Channel	38.26531	-121.7838	9.7	17.7	340	33.1	0.86
Lindsey Slough	EAV	38.25902	-121.7926	9.2	17.1	338	33.3	0.44
Lindsey Slough	FAV	38.25952	-121.7975	11.3	18.3	330	30.7	1.34
Lindsey Slough	SAV	38.25978	-121.7923	11.2	17.2	340	33.9	1.25
Miner Slough	Channel	38.24232	-121.6617	9.4	14.9	125	24.4	1.18
Miner Slough	EAV	38.23414	-121.6692	9.0	14.7	123	36.5	0.28
Miner Slough	FAV	38.24394	-121.6636	4.0	15.4	136	13.0	3.8
Miner Slough	SAV	38.25687	-121.6527	8.3	16.5	130	10.7	1.9

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dense patches of invasive water hyacinth (*Eichhornia crassipes)*. Channel sampling occurred in major channels outside the vegetated wetlands, where the banks were reinforced with large concrete chunks and boulders (rip-rap). We planned to collect three samples per habitat type per area per time period, for a total of 18 sweep nets and 18 leaf packs per habitat type. However, SAV and FAV were not present at all areas in March, and not all leaf packs were recovered due to high flows, vandalism, and loss, which resulted in a reduced sample size.

Description of sampling methods

For all invertebrate sampling methods, we used 500 μm mesh nets and sieves to target macroinvertebrates. All samples were preserved in 70% ethanol dyed with rose Bengal. All sampling was conducted under the Interagency Ecological Program Section 7 Biological Opinion issued to the U.S. Bureau of Reclamation by U.S. Fish and Wildlife Service (USFWS) in 1996, and additional amendments directly from the USFWS to CDFW (file number 1-1-96-F-1 and 1-1-98-I-1296, IEP Program Element Number 2016–311). No state scientific collection permit was necessary because all staff members were employees of CDFW (Fish and Game Code Section 1001). Before collection of each sample, we measured surface water temperature, specific conductance, and dissolved oxygen using a YSI Proplus sonde (YSI, Inc. Yellow Springs, OH), measured turbidity using a Micro TPW turbidity meter (HF Scientific, Inc.), and measured water depth using a boat-mounted Lowrance sonar (Lowrance Electronics, Tulsa, OK).

Sweep nets: We used a 25 cm x 30 cm d-frame net with 500 μm mesh for all sweep net samples. At each station, we collected three replicate samples, at least five meters apart. We adapted the sweep net technique slightly for different habitat types.

Channel (rip-rap): Five 1 m sweeps approximately 3 cm above the substrate.

EAV: Five 1 m sweeps, scraping the vegetation as much as possible to knock invertebrates off the stems.

SAV: Five 1 m sweeps through the thickest growth, collecting vegetation remaining within the net frame at the end of the sweep.

FAV: Net was lifted from beneath a clump of *Eichhornia*. Plant material outside of the net frame, and any leaves above the surface of the water, were severed from the sample with shears, leaving roots and associated invertebrates (similar to [47]).

Leaf packs: Tules (*Schoenoplectus acutus)* were harvested and dried to constant weight at 60˚C. Each leaf pack consisted of 30 g of dried stems (each approximately 15 cm in length) in a labeled, plastic mesh bag with 1 cm stretch mesh. This mesh was wide enough to allow all macroinvertebrates of interest to enter without allowing the stems to escape. These samplers were suspended in the midst of the vegetation for EAV, FAV, and SAV samples, and pinned on the bottom in channel habitat. Leaf packs were deployed February 2 and collected March 16 and 17, simultaneously with sweep net sampling. A second set of leaf packs were deployed March 16th and 17th, and collected at the same time as sweep net sampling May 2 and 3. During collection, leaf packs were surrounded with a 500 μm mesh net to retain macroinvertebrates.

Laboratory methods

Preserved invertebrates were counted and identified to varying taxonomic levels, according to their importance in fish diets, then grouped into larger taxonomic groupings (Order or Class) for analysis. Importance to fish diets was determined through extensive literature review of salmon and Delta Smelt diets from the area and similar estuaries [3, 48–51]. All terrestrial invertebrates were grouped into a single “terrestrial” classification. Insects with both aquatic and terrestrial life stages were classified by life stage, with the terrestrial adults grouped into the "terrestrial" classification and the aquatic larvae classified by Order. While our sampling methods targeted epibenthic and epiphytic invertebrates, samples also included larger zooplankton such as copepods and cladocerans, which were included in the analyses due to their importance in fish diets. If less than 400 individuals were present in a sample, the entire sample was identified. If more than 400 individuals were present, or more than four hours were required for processing, the invertebrates were quantitatively sub-sampled using a grid tray. We counted at least 400 organisms to achieve a precision of +/- 10%, as suggested by Harris et al. [52].

Analysis

To determine which sampler type had higher within-station variability, we compared coefficient of variation in total catch between the two groups using Bartlett's K-squared test. We compared total catch and taxa richness of the sampler types across habitat types and areas using generalized linear mixed models (GLMMs). For total catch, we used a GLMM with a negative binomial distribution and a log link, recommended for overdispersed count data, with the predictor variables listed in Table 2. For taxa richness, we used a normal distribution with an identity link and the same set of predictor variables. These analyses was performed using Program R version 3.4.1[53], packages glmmTMB [54] and lme4 [55].

To detect differences in community composition, we calculated the percent relative abundance of each taxon in each sample and used non-metric multidimensional scaling (NMDS) to visualize degree of overlap between communities. We performed a permutational multivariate analysis of variance (PERMANOVA) on the Bray-Curtis dissimilarity indices, using habitat type, sampler type, and area to test for statistical differences in community composition (Table 1) with R package vegan [56]. Permutations were stratified within area/habitat combinations.

The effect sizes and degrees of freedom calculated from the above analyses were used in a power analysis to determine minimum number of samples for each sampler type necessary to differentiate total catch and community composition between habitat types and areas using R package pwr [57].

To identify which taxa were most strongly associated with certain sampling methods, areas, and habitat types, we calculated the point-biserial correlation coefficient (r_{pb}) for each taxon, and tested coefficients' significance using the multipatt function in the R package indicspecies [58]. This statistical technique takes both frequency of occurrence and abundance into account in assigning which taxa are most closely associated with certain variables.

Results

Comparison of sweep nets and leaf packs

We recovered 60 of the 72 (83%) deployed leaf packs. Losses during deployment occurred due to vandalism, high flows, or stranding above the high-water mark. In contrast, 66 of the 67

Table 2. Predictor variables for explaining observed differences in catch and taxa richness.

Variable	Description
Habitat type	EAV, SAV, FAV, or rip-rapped channel bank
Sampler type	Leaf pack or sweep net
Sampler*Habitat	Interaction between sampler type and habitat type
Month	March or May
Error(Area/Habitat)	Error term: Habitat type crossed with Area

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(98.5%) sweep net samples were successfully collected. This gave us a total of 126 samples with 38,032 individual organisms which we divided into 25 taxa (see S1 Data).

Sweep nets had a significantly higher coefficient of variation in total catch than leaf packs (1.53 versus 1.17, Bartlett's K-squared: 160.9, P value <0.001). The variance in total catch for sweep nets was also higher than leaf packs (Bartlett's K-squared: 32.39, P value <0.001). Non-homogeneous variances made the data inappropriate for parametric statistics, however, a Kruskal-Wallace test showed that total catch was not significantly different between the two sampler types (test statistic: 0.087, P value: 0.767).

Total catch and taxa richness

There was a significant difference in total catch for the different habitat types, and a significant interaction between habitat type and sampling method. In particular, SAV samples had higher catch than channel and EAV samples (Fig 2, Table 3), and sweep net samples in FAV had a higher total catch than sweep net samples in other habitat types. There was no difference in abundance between March and May, nor was there a significant main-effect of sampling method (Table 3). Post-hoc power analyses of the model of total catch showed that 30 sweep net samples were needed to achieve 80% power at a 0.05 significance level for the overall model, whereas only 13 leaf pack samples were needed.

There was also a significant effect of habitat type on taxa richness. Sweep nets had higher taxa richness than leaf packs, and SAV and FAV samples had higher richness than channel or EAV samples (Fig 3, Table 4). There was no difference in taxa richness between months, and there was no significant interaction between sampler type and habitat type.

Community composition

Community composition also varied between habitat types and between areas. An overall PERMANOVA showed that there were significant differences between habitat type, sampler

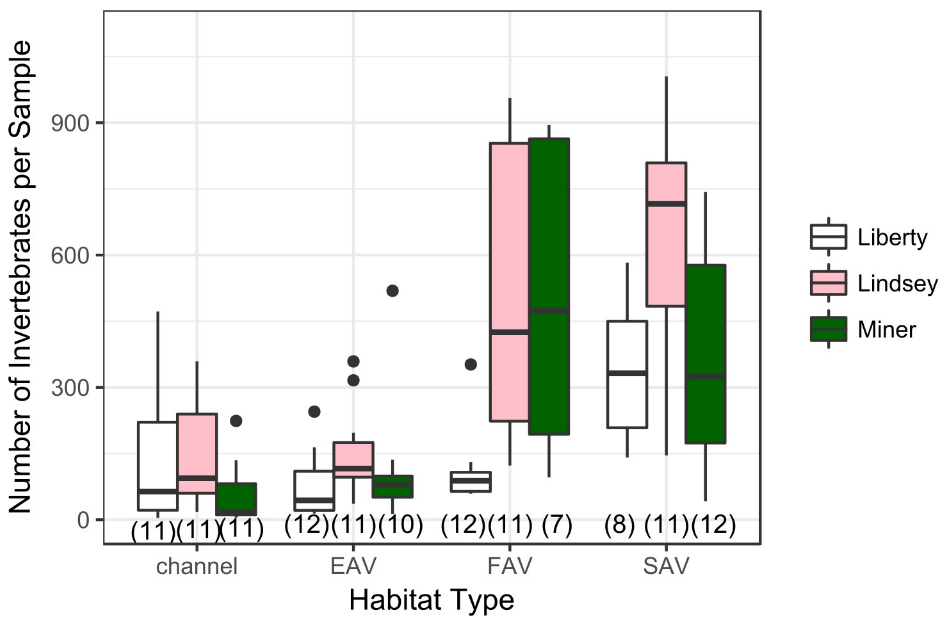

Fig 2. Distribution of total catch in each area and habitat type. Sample size in parentheses below boxes. Four outliers in FAV and SAV samples with catch > 1000 not shown. Models support significantly higher catch in SAV than in other habitats and significantly higher catch with the sweep net in FAV (see Table 3).

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Table 3. Coefficients for the negative binomial mixed model with a log link predicting total invertebrate catch of sweep nets and leaf packs Model: Catch ~ Habitat*Sampler + Month + Error(Area/Habitat).

Factor	Estimate	Std. Error	z value	P value	
Fixed effects:					
Intercept: Channel, Leaf pack, March	5.087	0.297	17.130	<0.0001	**
Habitat: EAV	-0.042	0.329	-0.128	0.898	
Habitat: FAV	0.555	0.315	1.761	0.078	
Habitat: SAV	1.235	0.287	4.302	<0.0001	**
Sampler: Sweep net	-0.248	0.310	-0.802	0.423	
Month: May	-0.126	0.132	-0.954	0.340	
EAV*Sweep net	0.427	0.427	0.999	0.318	
FAV*Sweep net	0.887	0.394	2.254	0.024	*
SAV*Sweep net	-0.046	0.377	-0.121	0.904	
Random effects:	**Variance**	**St. Dev.**			
Habitat*Area	0.0234	0.1534			
Area	0.0855	0.2925			

* significant P value, $P < 0.05$

** highly significant P value, $P < 0.005$

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type, and area, though not between months. However, pairwise comparisons of PERMANOVA results indicate that sweep nets show significant differences between areas as well as between habitat types, whereas leaf pack samples only had differences between areas and did not show differences between habitat types (Table 5, Fig 4). This can be seen on the NMDS plots, where ellipses surrounding the standard devidation of habitat type centroids have a much higher degree of overlap than hulls surrounding areas (Fig 5A), and the consistent

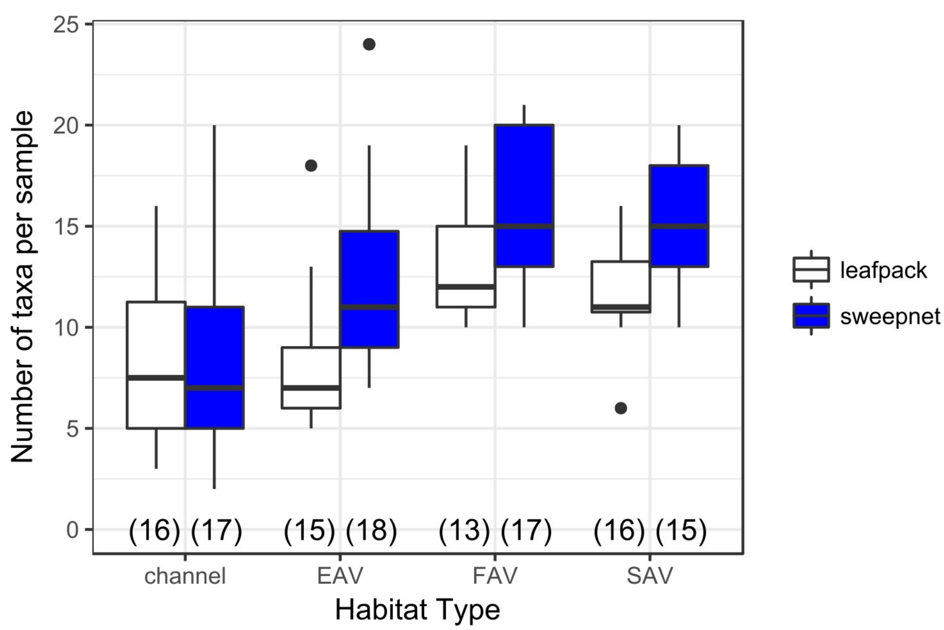

Fig 3. Distribution of taxa richness for sweep nets and leaf packs in various habitat types. Sample size is in parentheses along the x-axis. Models support significantly higher richness for samples collected with sweep nets, and significantly higher richness for FAV and SAV samples than EAV or channel samples.

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Table 4. Coefficients for the linear mixed model predicting taxa richness of sweep nets and leaf packs Model: Catch ~ Habitat + Sampletype + Month + Error(Area/Habitat). The interaction term was not significant and so was dropped from the final model.

Factor	Estimate	Std. Error	df	t value	P value	
Fixed effects:						
(Intercept: Channel, Leaf pack, March)	7.420	1.062	12.598	6.984	<0.0001	**
Habitat: EAV	2.161	1.317	7.517	1.640	0.142	
Habitat: FAV	5.866	1.339	7.898	4.380	0.002	**
Habitat: SAV	4.860	1.336	7.881	3.638	0.007	*
Sampler: Sweep net	2.838	0.706	115.055	4.020	<0.0001	**
Month: May	-0.418	0.715	114.846	-0.584	0.560	
Random Effects:	**Variance**	**St. Dev.**				
Habitat*Area	1.183	1.088				
Area	4.444e-9	6.667e-5				

* significant p-value, $P < 0.05$

** highly significant p-value, $P < 0.005$

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dominance of particular taxonomic groups among habitat types for each area (Fig 4). Post-hoc power analyses of the PERMANOVA results showed that 29 sweep net samples were needed to achieve 80% power at a 0.05 significance level for differences between habitat types, whereas 60 leaf pack samples were needed.

Analysis of point-biserial correlation coefficients highlight which taxa drove the observed difference in overall community composition between sample types, areas and habitat types (Table 6). Leaf packs were associated with three more sedentary epifaunal taxa, whereas sweep nets were associated with nine highly mobile taxa, including zooplankton and fish (Table 6). There were four

Table 5. Results of PERMANOVA performed on the entire data set and on subsets of the dataset using sweep nets only or leaf packs only.

A) Overall PERMANOVA						
Factor	**DF**	**Sum of Sqs.**	**Mean Sqs.**	**F value**	**R^2**	**P value**
Habitat type	3	2.003	0.668	3.33	0.155	0.001**
Sample type	1	1.184	1.184	5.905	0.092	0.001**
Area	2	1.814	0.907	4.523	0.140	0.001**
Sample type* Habitat type	3	0.638	0.213	1.183	0.055	0.285
Residuals	36	7.219	0.201		0.558	
A) Leaf packs only						
Factor	**DF**	**Sum of Sqs.**	**Mean Sqs.**	**F value**	**R^2**	**P value**
Habitat Type	3	0.904	0.301	1.533	0.157	0.107
Area	2	1.503	0.752	3.825	0.261	0.001**
Residuals	17	3.341	0.196		0.581	
B) Sweep nets only						
Factor	**DF**	**Sum of Sqs.**	**Mean Sqs.**	**F value**	**R^2**	**P value**
Habitat Type	2	0.9532	0.477	2.554	0.161	0.011*
Area	3	1.801	0.600	3.217	0.303	0.003**
Residuals	17	3.172	0.187		0.535	

* significant p-value, $P < 0.05$

** highly significant p-value, $P < 0.005$

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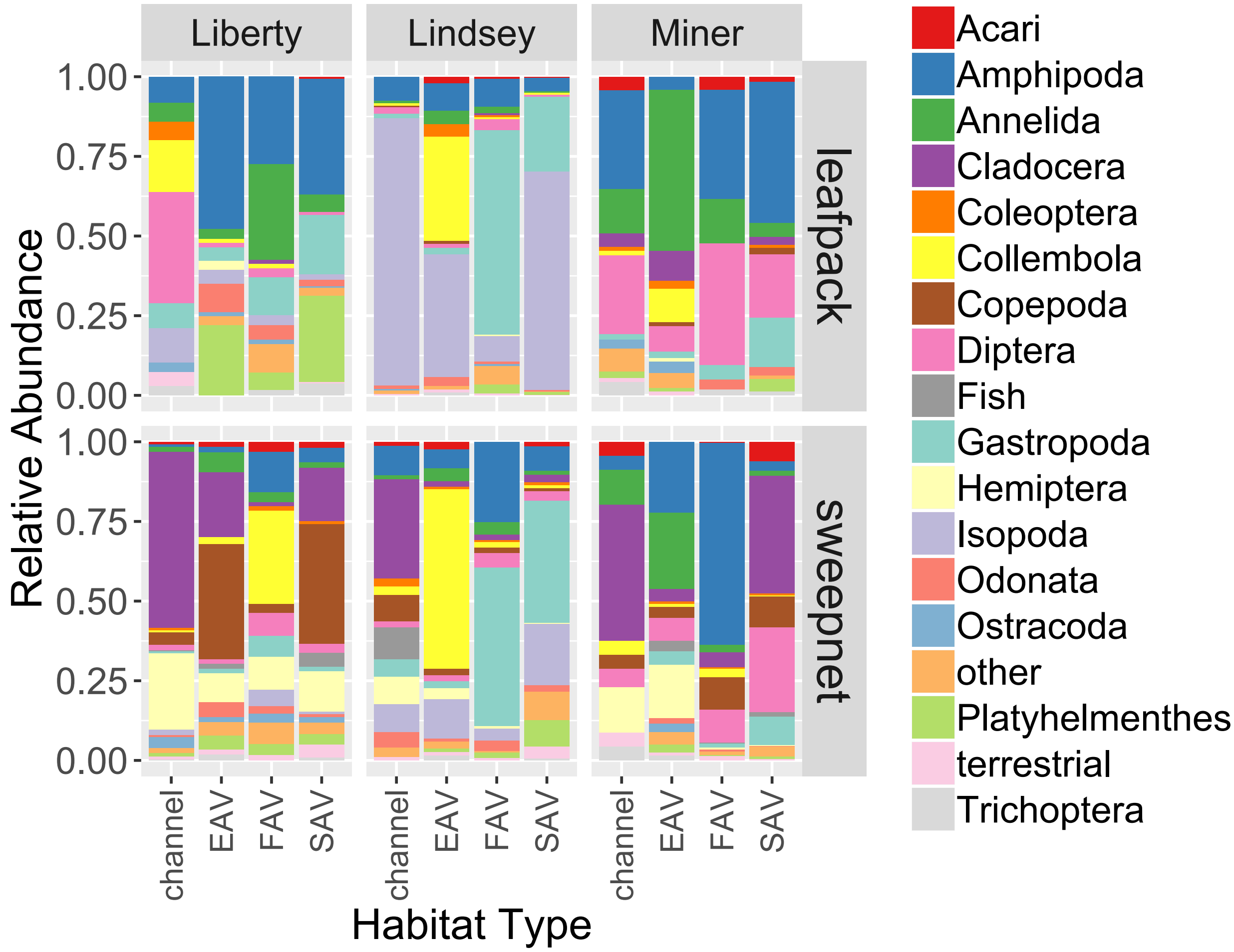

Fig 4. Relative abundance of major taxa in samples collected with leaf packs and sweep nets in various habitats in the three different areas (Liberty, Lindsey, and Miner). Taxa that made up less than 0.5% of the total catch were combined into the "other" category to simplify the graph. PERMANOVA showed significant differences between habitat types, between areas, and between sample types (Table 5). The "fish" category included juvenile sunfish (family Centrarchidae), Mississippi silversides (*Menidia beryllina*), and gobies (genus *Tridentiger*), all non-native species.

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taxa associated with Lindsey Slough, whereas Miner Slough and Liberty Island each had two taxa (Table 7). There were no taxa associated with channel habitat over the other habitats. One taxon (Collembola) was associated with EAV, three taxa with FAV, and four taxa with SAV (Table 8).

Discussion

Choosing sampling methods

We found that sweep nets were more effective and efficient than leaf packs in sampling a variety of shallow water habitats in the Sacramento-San Joaquin Delta for macroinvertebrate taxa valuable in diets of key fish species. Sweep nets required a single trip to the field, and did not require assembly ahead of time, making them a considerably lower investment in staff time. While sweep nets had higher variability in total catch than leaf packs, and thus required greater sample sizes to compare catch between groups, they were more cost effective, were less subject to loss or vandalism, were better able to distinguish differences in diversity between habitat types (Fig 5), and had higher taxa richness (Fig 3, Table 4). They also required fewer samples

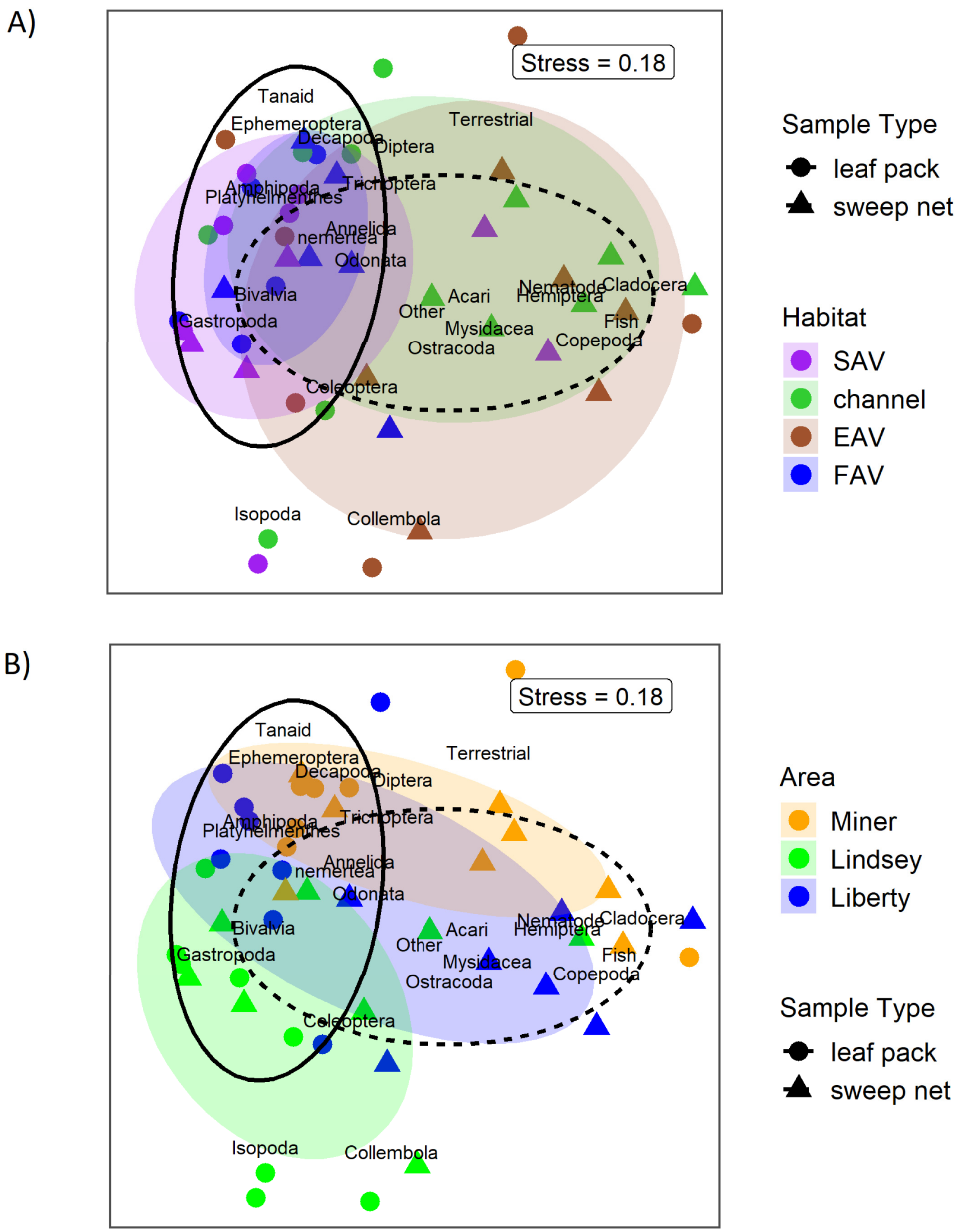

Fig 5. **A)** Non-metric multidimentional scaling plots (NMDS) of propotional taxonomic abundance with colored elipses showing the standard deviation of group centroids by habitat type and black outlined elipses showing grouping by sample type. Points represent samples, text represents species. Stress = 0.18. **B)** Plot of the same NMDS as 5A, but with colored elipses showing the standard deviation of group centroids by Area. Black outlined elipses show grouping by sample type.

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Table 6. Taxa which were significantly associated with a particular sample type, area, or habitat, mean abundance by group (abund.), proportion of samples where taxa was present (pres.), and statistical significance of the association.

	Leaf pack		*Sweep net*				
Indicator taxa	**abund.**	**pres.**	**abund.**	**pres.**	**association**	r_{pb}	**P value**
Isopoda	70.12	0.58	8.18	0.43	Leaf pack	0.202	0.005*
Platyhelminthes	7.08	0.50	2.55	0.43	Leaf pack	0.179	0.05*
Trichoptera	1.00	0.30	0.31	0.19	Leaf pack	0.17	0.039*
Acari	0.28	0.17	2.48	0.42	Sweep net	0.168	0.003**
Cladocera	0.38	0.13	32.72	0.78	Sweep net	0.293	0.001**
Collembola	3.58	0.32	13.28	0.49	Sweep net	0.181	0.044*
Coleoptera	0.28	0.17	1.27	0.43	Sweep net	0.284	0.001**
Copepoda	0.18	0.10	21.91	0.78	Sweep net	0.34	0.001**
Diptera	0.28	0.78	35.31	0.82	Sweep net	0.195	0.015*
Fish	0.00	0.00	0.73	0.19	Sweep net	0.202	0.001**
Hemiptera	0.08	0.07	8.76	0.57	Sweep net	0.264	0.001**
Terrestrial	0.43	0.30	2.89	0.45	Sweep net	0.285	0.001**

* significant p-value, $P < 0.05$

** highly significant p-value, $P < 0.05$

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than leaf packs to characterize community composition. Within the taxa captured by leaf packs, only two taxa were found to be more strongly associated with leaf packs than sweep nets, whereas nine taxa were more strongly associated with sweep nets (Table 6). Therefore, few taxa will be missed by choosing sweep nets over leaf packs. Furthermore, the insects and Cladocera associated with sweep nets are considered highly important for salmonid diets, whereas the Isopoda and Platyhelminthes associated with leaf packs rarely occur in at-risk fish diets during the life stages found in freshwater wetlands [48–50].

Our results are consistent with research findings from other areas in which active methods, such as sweep nets, gave a more accurate view of community composition than substrate colonization traps [31, 59]. Sweep nets have also been found to better differentiate between habitat types within a wetland than other sampler types [60]. However, both these sampling methods

Table 7. Taxa which were significantly associated with a particular area mean abundance by group (abund.), proportion of samples where taxa was present (pres.), and statistical significance of the association.

	Liberty		*Lindsey*		*Miner*				
Indicator taxa	**abund.**	**pres.**	**abund.**	**pres.**	**abund.**	**pres.**	**association**	r_{pb}	**P value**
Collembola	18.25	0.35	64.36	0.61	9.67	0.25	Lindsey	0.316	0.001**
Coleoptera	2.60	0.19	5.45	0.41	4.83	0.33	Lindsey	0.229	0.026*
Gastropoda	52.69	0.72	591.50	0.89	74.15	0.78	Lindsey	0.322	0.001**
Isopoda	5.92	0.51	292.38	0.95	0.00	0.00	Lindsey	0.339	0.001**
Odonata	7.50	0.51	9.93	0.61	3.50	0.25	Lindsey	0.242	0.011*
Decapoda	1.00	0.02	0.00	0.00	3.50	0.10	Miner	0.215	0.022*
Diptera	13.93	0.67	35.33	0.80	154.87	0.95	Miner	0.365	0.001**
Hemiptera	52.38	0.42	7.57	0.27	15.00	0.30	Liberty	0.215	0.034*
Platyhelminthes	33.25	0.58	18.11	0.43	4.25	0.38	Liberty	0.267	0.005*

* significant p-value, $P < 0.05$

** highly significant p-value, $P < 0.05$

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Table 8. Taxa which were significantly associated with a particular habitat, mean abundance by group (abund.), proportion of samples where taxa was present (pres.), and statistical significance of the association.

	Channel		*EAV*		*FAV*		*SAV*				
Indicator taxa	**abund.**	**pres.**	**abund.**	**pres.**	**abund.**	**pres**	**abund.**	**pres.**	**association**	r_{pb}	**P value**
Collembola	3.50	0.36	95.22	0.55	29.71	0.57	3.00	0.16	EAV	0.374	0.001**
Amphipoda	51.67	0.76	77.45	0.85	613.6	0.93	256.3	0.90	FAV	0.354	0.001**
Gastropoda	8.33	0.55	15.36	0.73	584.4	1.00	403.7	0.94	FAV	0.239	0.021*
Terrestrial	3.25	0.39	3.29	0.36	22.00	0.40	8.71	0.35	FAV	0.241	0.034*
Acari	2.40	0.21	3.20	0.21	2.60	0.23	15.78	0.55	SAV	0.266	0.005*
Isopoda	130.6	0.45	63.33	0.45	23.88	0.63	448.4	0.48	SAV	0.244	0.037*
Platyhelminthes	3.75	0.21	15.86	0.39	7.63	0.47	40.90	0.81	SAV	0.389	0.001**
Trichoptera	3.40	0.18	2.60	0.21	1.67	0.13	6.57	0.45	SAV	0.245	0.029*

* significant p-value, $P < 0.05$

** highly significant p-value, $P < 0.05$

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have some biases. Leaf packs sample a much lower volume than sweep nets, which may partially explain their lower overall taxonomic richess. However, sweep nets may preferentially sample mobile organisms, missing shredders and detritivores. The use of sweep nets should be standardized as much as possible using published protocols, such as those recommended by International Organization for Standardization (ISO 10870:2012) [61]. Neither sweep nets nor leaf packs will adequately characterize terrestrial fall-out invertebrates or benthic infauna. Furthermore, the patchiness inherent in invertebrate communities may mean that multiple sampling types may be needed for certain types of questions.

In particular, higher sample size is usually necessary to describe differences in invertebrate density and biomass than to describe differences in diversity (as suggested by [62]), so there may be some situations where sweep nets are too highly variable to allow differentiation between areas without a significant increase in sampling effort. In this case, leaf packs may be a valuable alternate sampling method, since they have been used effectively to evaluate wetland restoration in other systems [39]. Similar catch, despite different sampling volume between methods indicates leaf packs may sample more individuals of the representative taxa. Furthermore, passive samplers may be more sensitive to different stressors than active methods [31] and may be more appropriate to answer other questions besides relative abundance of invertebrates important for of fish food. However, leaf packs should only be used in emergent vegetation where they most accurately replicate the surrounding habitat and are least likely to be lost.

Comparing diversity across habitat types

With both sampling methods combined, we gained a better understanding of how invertebrate communities vary across freshwater wetland habitat types.

Emergent aquatic vegetation. Emergent vegetation was once the dominant habitat type in the Delta [6], so restoration of this habitat type may provide the best resources for native species. We found a wide variety of taxa in EAV, including Diptera, Hemiptera, and Amphipoda (Fig 4). Collembola were strongly associated with this habitat type, more so than any other habitat (Table 8). Previous research in the Delta has focused on pelagic invertebrates and open water fish habitat, so there are few local studies of EAV communities with which to compare our results. However, two studies using fall-out traps and neuston tows near EAV in the Delta also found high abundances of Collembola and Diptera [2, 63].

Diptera, Hemiptera, Amphipoda, and Collembola are all important components of fish diets in other estuaries, particularly for juveniles salmonids [51, 64, 65]. Studies of fish diets from vegetated tidal wetlands in the Delta are scarce, but Sommer et al. [50] found that salmon on the nearby Yolo Bypass floodplain derived the majority of their diets from chironomid midges (Diptera), which are plentiful in EAV (Fig 4). Delta Smelt also appear to consume more insects and amphipods when captured in areas with more EAV [48, 66]. The lack of comparable studies highlights the need for increased research and monitoring in areas of EAV adjacent to future restoration sites.

Floating aquatic vegetation. Invasive FAV is actively controlled in the Delta, and many studies have documented the negative impact of *Eichhornia* on water chemistry, water flow, and boat traffic (as reviewed in [25]). However, FAV's effect on the invertebrate community is understudied. We found a high abundance of invertebrates (Table 2, Fig 2), and found strong associations between FAV and terrestrial invertebrates (Table 5C). We also found strong associations for Amphipoda and Gastropoda, and high abundances of Diptera larvae, similar to other studies of *Eichhornia* in the Delta [27, 47].

While floating vegetation is not considered good habitat for native fishes, the invertebrates we found in this habitat may be an important resource. Terrestrial invertebrates are often an important component of salmonid diets [65], and Amphipoda and Diptera provide particularly high-energy food for at-risk fishes [51]. The benefits of these fish-food invertebrates may help offset the water quality problems associated with *Eichhornia*; however, native species of floating vegetation, such as *Hydrocotyle*, often have a higher overall diversity of invertebrates and higher proportion of native invertebrates [27].

Submerged aquatic vegetation. Like FAV, SAV is actively controlled, but few researchers have assessed its invertebrate communities. We found strong associations between SAV and Isopoda, Platyhelminthes, Acari, and Trichoptera (Table 5C), and also found high abundances of Amphipoda, and Diptera (Fig 4). Boyer et al. [26] compared invertebrate communities on *Egeria densa* and *Stuckenia* spp. in Suisun Bay and the western Delta, finding similarly high abundances of Amphipoda, Isopoda, Gastropoda, and Diptera [26]. A similar study by Young et al. [28] in the central Delta that looked at a wider variety of SAV species also found catches dominated by Amphipoda, Diptera, and Gastropoda, though found fewer Isopoda.

Amphipoda and Diptera may be particularly important in salmonid diets [50, 65], so SAV may provide a source of fish food, if the fishes can access it. However, recent expansions of *Egeria* and other invasive SAV in the Delta have been linked to reduced turbidity and increased habitat for non-native piscivores [22–24]. Fish often have decreased foraging success in vegetated habitats [22, 67] and *Egeria densa* decreases foraging success more than other species of SAV [28]. This may decrease non-native piscivores' ability to prey on native species, but also may decrease the foraging success of native species. Whether increased invertebrate abundance in SAV will offset the negative impacts remains to be seen.

Channel habitat. Channel habitat, dominated by rip-rapped banks, is the dominant habitat type in the present Delta ecosystem [6]. Restoration aims to decrease the area of reinforced banks, replacing them with shallow, sloping banks, setback levees, and vegetated benches [68]. There was no significant difference in total catch of invertebrates between channel habitat and EAV (Fig 2, Table 3); however, there was lower taxonomic richness in channel habitat, and the habitats had different community compositions (Figs 3 and 4). We found a relatively high proportion of zooplankton, particularly Copepoda and Cladocera, in these samples (Fig 4), but no taxa uniquely associated with channel habitat (Table 6). Neither sweep nets nor leaf packs are generally used for zooplankton (such as copepods and cladocerans), so other methods, such as trawled zooplankton nets, may be better suited to sample this type of open-water habitat. However, inclusion of some of these taxa in our sweep-net samples show that we can use sweep nets to directly compare channel habitat to vegetated habitat, at least at the level of presence-absence.

Copepoda and Cladocera are commonly found in salmon and smelt diets [49, 50]. However, these organisms are, on average, smaller and less nutritious than the amphipods common in emergent vegetation [51]. Because all the taxa present in the channel were also found in the other habitat types in similar abundances, this habitat does not appear to provide unique resources for fish. Furthermore, channel habitats are often characterized by rip-rapped banks and man-made structures where predatory fish, such as Striped Bass congregate [69].

Invertebrate diversity across areas

There were strong differences in community composition among the three sampling areas (Figs 2, 3 and 4), despite all being within ten miles of each other, and in similar sized sloughs. This is in contrast to Simenstad et al. [70], who found relatively small differences in invertebrate communities between areas in the Delta that were much more widely distributed. Thompson et al. [71], found benthic communities in the Delta could be categorized into at least three clusters, though these were based on habitat characteristics (sediment type, vegetation, depth), rather than location *per se*. Other studies of shallow-water habitat in the Delta have found significant differences in phytoplankton and benthic invertebrate biomass that can be traced to tidal transport processes, basin geometry, and benthic substrate [2, 72].

In our study, flow from the Sacramento River greatly influenced water quality on Miner Slough, providing lower turbidity, cooler water, and higher flows than the other two areas (Table 1)[73]. This area provided more decapod crustaceans and Diptera larvae (Table 7). As a backwater slough, Lindsey Slough had lower flows and longer residence time, characteristics that have been implicated in increased zooplankton productivity [73], which may also apply to other invertebrates [74]. Lindsey Slough had strong associations with Isopoda, Odonata, Coleoptera, and Collembola (Table 5B). Liberty Island's primary water source is the Yolo Bypass floodplain, which may be a higher source of primary phytoplankton productivity than riverine water [75]. However, the organisms associated with this area were Platyhelminthes and Hemiptera (Table 7), neither of which directly feed on phytoplankton. Liberty Island also has a much larger area of open water adjacent to our sampling areas than the other two areas, with the potential for increased wind-waves and phytoplankton productivity, which may impact invertebrate abundance [76]. Our observed area differences may be due to habitat factors not included in our models, such as water velocity, water source, substrate type, and average depth, but the current study had too small a sample size to include these as parameters. Further research is necessary to tease apart potential causes for these differences.

Restoration implications

We found significant differences in macroinvertebrate communities that may be traced to habitat heterogeneity. This implies that constructing a diverse range of habitats, including emergent vegetation, floating vegetation, submerged vegetation, and open water, during tidal wetland restoration may increase the variety of invertebrates produced on the site. The difference in invertebrates between habitats is not surprising, as research in this and other systems have found large differences between habitats [2, 30, 71], but it does give restoration practitioners important information on how fish may use the sites. Fish have dietary preferences, but many fishes shift their diets with the abundance of local resources [77]. For example, Mississippi Silversides collected on Liberty Island were found to consume more amphipods in open water and more insects in vegetated habitat [48]. Delta Smelt collected in deep channels were found to consume less than 5% amphipods (by weight), and not enough insects to report

[49]. However, smelt collected on Liberty Island, where more vegetated habitat is available, consumed 14% amphipods and 15% insects [48]. An increase in invertebrates associated with vegetation as part of wetland restoration may help ameliorate declines in the pelagic zooplankton that often make up the majority of smelt diets [78, 79].

A wider range of invertebrate prey may increase resiliency of at-risk fishes and the ecosystem as a whole. There are multiple ways a diverse ecosystem may respond to changes in taxon composition [80], but there is broad consensus that decreased diversity will decrease food web stability and resilience to change [81, 82]. While restoring many different types of tidal wetland habitats alone is unlikely to reverse the declines of at-risk fishes, the increase in food web stability provided by wetlands may increase their resilience to other stressors and future disturbances [15, 83]. Differences in invertebrate similarity among areas and habitats stress the importance of restoring habitat diversity. Within a restoration site, construction of multiple habitat types may be more beneficial than a single habitat type that is believed to be most important to at-risk species at the time the site is built. We found major differences in communities across areas that were relatively close together, and restoration sites spread across the Delta have the potential to provide even higher differences in diversity. However, connectivity between these restoration sites will be essential for migratory species to access all of these diverse resources [15, 68], and for long-term population and community stability [5, 84].

Surprisingly, we found no significant differences in invertebrate catch between the two time periods (March versus May). This suggests that invertebrate abundance may remain somewhat constant throughout the spring, however further sample points are required before any conclusions can be drawn. Due to strong seasonal patterns in invertebrate communities found by other studies [2, 40, 85], further research will be necessary to characterize year-round invertebrate communities.

Conclusion

Invertebrate community composition was highly variable within and between Delta wetlands. Sweep nets provided a simple, efficient way to sample the invertebrate community, and demonstrated that different areas and habitat types supported different groups of organisms. Measuring invertebrate abundance across all habitat types within a wetland will allow managers to evaluate the effectiveness of their restoration projects in providing food for at-risk fishes. Wetland restoration can benefit from incorporating multiple habitat types in each project to develop a diverse community of invertebrates. Furthermore, restoration projects in different areas may have different benefits, and a variety of restoration projects may provide greatest resilience for the aquatic food web and the at-risk fishes it supports.

Supporting information

S1 Data. Catch of each taxonomic group of invertebrates used for the anlaysis of this data.
(CSV)

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