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Macroinvertebrate Prey Availability and Fish Diet Selectivity in Relation to Environmental Variables in Natural and Restoring North San Francisco Bay Tidal Marsh Channels

Emily R. Howe^{*1}, Charles A. Simenstad¹, Jason D. Toft¹, Jeffrey R. Cordell¹, and Stephen M. Bollens²

ABSTRACT

Tidal marsh wetlands provide important foraging habitat for a variety of estuarine fishes. Prey organisms include benthic/epibenthic macroinvertebrates, neustonic arthropods, and zooplankton. Little is known about the abundance and distribution of interior marsh macroinvertebrate communities in the San Francisco Estuary (estuary). We describe seasonal, regional, and site variation in the composition and abundance of neuston and benthic/epibenthic macroinvertebrates that inhabit tidal marsh channels, and relate these patterns to environmental conditions. We also describe spatial and temporal variation in diets of marsh-associated inland silverside, yellowfin goby, and western mosquitofish. Fish and invertebrates were sampled quarterly from October 2003 to June 2005 at six marsh sites located in three river systems of the northern estuary: Petaluma River, Napa River, and the west Delta. Benthic/epibenthic macroinvertebrates and neuston responded to environmental variables related to seasonal changes (i.e., temperature, salinity), as well as those related to marsh structure (i.e., vegetation, channel edge). The greatest varia-

tion in abundance occurred seasonally for neuston and spatially for benthic/epibenthic organisms, suggesting that each community responds to different environmental drivers. Benthic/epibenthic invertebrate abundance and diversity was lowest in the west Delta, and increased with increasing salinity. Insect abundance increased during the spring and summer, while Collembolan (springtail) abundance increased during the winter. Benthic/epibenthic macroinvertebrates dominated fish diets, supplemented by insects, with zooplankton playing a minor role. Diet compositions of the three fish species overlapped considerably, with strong selection indicated for epibenthic crustaceans—a surprising result given the typical classification of *Menidia beryllina* as a planktivore, *Acanthogobius flavimanus* as a benthic predator, and *Gambusia affinis* as a larvivorous surface-feeder. Fish diets were influenced by position along the estuarine gradient and season. Overall, our data show that local-scale site effects and marsh position within the estuary influence invertebrate community composition and abundance. Additionally, we show that restoring marsh ecosystems can subsidize fishes similarly to reference marshes. We thus recommend that managers focus on the ability of restoring marshes to produce food subsidies for target species when planning and designing tidal marsh restoration projects, especially those targeted for food web support.

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KEY WORDS

Tidal marsh, macroinvertebrate ecology, fish ecology, estuarine ecology, community composition, tidal marsh restoration, San Francisco Estuary

INTRODUCTION

Worldwide, tidal marsh degradation has decreased estuarine ecosystem functions such as energy production, fish and wildlife habitats, nutrient cycling and filtration, and integrity of food web systems (Teal 1962; Childers et al. 2002; Deegan et al. 2002; Kemp et al. 2005; Van Dolah et al. 2008). In the San Francisco Estuary (estuary), rapid and extreme structural and hydrological modifications by human activity over the past 150 years have dramatically altered the estuarine landscape, where all but 85 km² of the once vast (2,200 km²) complex of wetlands and tidal marshes have been leveed or filled for development projects and agriculture (Atwater et al. 1979). The estuary historically supported large populations of migrating waterfowl, marine mammals, and productive fisheries, including sardines, herring, halibut, sturgeon, oyster, crab, shrimp and salmon (Skinner 1962). Today, the Bay-Delta system no longer supports such a breadth or abundance of organisms, and the diversity and productivity of the historic food web has declined. Most recently, an unexpected decline in the abundance of several pelagic nekton species—commonly referred to as the Pelagic Organism Decline (POD)—has been observed, possibly triggered by a combination of food stress, increased pollution, biological invasions, hydrological changes in freshwater inflow, and physical-chemical changes to pelagic fish habitat (Sommer et al. 2007). However, the loss of wetlands and tidal marshes is typically missing from conceptual models that describe potential contributors to the POD (Sommer et al. 2007), even though that loss may be an underlying contributor to present-day food limitation.

Tidal marsh wetlands have been identified as crucial habitat for many estuarine species, partially because of high productivity and dense prey resources

(Wouters and Cabral 2009). In the estuary, not only do native, resident, and at-risk species rely on tidal marsh ecosystems, but a number of transient species traditionally described as pelagic use marsh-derived resources as well (Gewant and Bollens 2011; S.M. Bollens, WSU, unpublished data, 2013). Recent work indicates that the diets of marsh-associated fish comprise benthic, epibenthic, planktonic, and neustonic invertebrates (unpublished BREACH data; Toft et al. 2003; Visintainer et al. 2006; Cohen and Bollens 2008; Whitley and Bollens 2013). Combined with stable isotope food web assessments, these stomach content-based studies confirm that the macroinvertebrate community plays a crucial role as primary consumers in the estuary, translating marsh-derived detritus to higher trophic levels, including fish, birds, and mammals (Grenier 2004; Grimaldo et al. 2009; Howe and Simenstad 2011). The marsh-associated macroinvertebrate community is therefore potentially critical to sustaining the productivity of many fish populations in the estuary, although several studies from the interior Delta do not indicate that marsh ecosystems in that region of the estuary are crucial for native fish (Nobriga et al. 2005; Brown and Michnuik 2007; Grimaldo et al. 2004, 2012). Thus, understanding the trophic role of tidal marsh ecosystems is of inherent interest, especially given that many of the species associated with the recent POD rear and spawn in the brackish and freshwater regions of the estuary where the remaining marsh ecosystems are most abundant (Sommer et al. 2007).

Invertebrate communities associated with tidal marsh ecosystems are largely ignored when food web support of the estuarine fish community in the estuary is characterized, despite their well-established role in the conditioning and transfer of marsh-derived energy to higher trophic levels in other systems (Teal 1962; Odum 1980; Cloern et al. 1985; Williams and Hamm 2001; Havens et al. 2002; Degraer et al. 2008; Tomiyama et al. 2008). Instead, the vast majority of scientific and management efforts in the estuary have focused on the role of the pelagic ecosystem in supporting metabolism in the estuary. As such, an extensive body of literature exists that describes

the relationship between physical environmental variables, phytoplankton production, and pelagic macroinvertebrate consumers such as zooplankton and micronekton in the estuary (e.g., Cloern et al. 1985; Kimmerer and Orsi 1996; Jassby et al. 2002; Kimmerer 2002; Jassby et al. 2003; Kimmerer 2004; Cloern and Dufford 2005; Gewant and Bollens 2005; Lopez et al. 2006; Cloern 2007; Bollens et al. 2011). Considerably less attention has been paid to shallow water marsh ecosystems since the finding that, unlike undisturbed estuaries, the estuary currently depends on phytoplankton as opposed to detrital inputs to drive the pelagic food web (Jassby and Cloern 2000; Jassby et al. 2003); a finding likely driven by the very small amount of remaining marsh ecosystems in the region. Given the importance of tidal marshes in supporting estuarine food webs in other systems, however, marsh-associated prey may also provide important food resources for estuary nekton.

Unfortunately, little is known about the spatial and temporal distribution and abundances of the macroinvertebrate marsh community in estuary. Elsewhere, studies show that estuarine benthic macroinvertebrates significantly respond to physical gradients, such as sediment grain size and salinity (Nanami et al. 2005; Degraer et al. 2008; Tomiyama et al. 2008). Other important environmental variables that influence the spatial distribution, composition, and abundance of estuarine benthic macroinvertebrate communities include the distance from the estuary mouth, exposure to fetch, relative elevation, submerged vegetation coverage, water temperature and dissolved oxygen concentration (Desmond et al. 2002; Degraer et al. 2008; Tomiyama et al. 2008; Valesini et al. 2010). While descriptions of zooplankton use of intertidal marsh channels and their ecological roles are rare (S.M. Bollens, WSU, unpublished data, 2013), evidence from the Yangtze River estuary suggests that spatial variation among zooplankton communities corresponds to changes in salinity, while temporal variation results from shifts in water temperature, chlorophyll α concentration, and pH (Zhou et al. 2009). Similarly, use of interior marsh channels by

neustonic invertebrates is rarely described, but more general studies on salt-marsh arthropod communities indicate that salinity, vegetation assemblage, vegetation coverage, and inundation regime strongly influence the abundance and assemblage structure of these organisms (Stocks and Grassle 2003; Petillon et al. 2008; Wu et al. 2009; Reynolds and Boyer 2010).

The complexity of marsh invertebrate community responses to the aforementioned environmental variables in other estuaries makes it difficult to translate these results to the estuary. In addition, there is also a high degree of uncertainty in the ability of restoration efforts to produce expected or desired responses (Simenstad et al. 2006). Many of the environmental variables that ostensibly influence marsh invertebrate communities can neither be planned for nor engineered in restoration efforts. For example, salinity presents a challenge because many restoration sites are situated opportunistically along the estuarine gradient. Sediment characteristics, such as grain size and accretion rates, are usually a function of landscape-scale processes (Ganju et al. 2005; Molinaroli et al. 2009), and cannot be permanently engineered into a specific restoration site. However, some structural components can be designed (van Proosdij et al. 2010), such as tidal prism, which has been shown to correlate with site size, marsh elevation, and tidal channel characteristics including sinuosity, density, complexity, cross-sectional area, and depth (Williams et al. 2002; Marani et al. 2003; D'Alpaos et al. 2006, 2010; Hood 2007). All of these factors have been shown to influence fish assemblage structure in tidal marsh environments (Minello et al. 1994; Minello and Rozas 2002; Visintainer et al. 2006; Gewant and Bollens 2011).

Given the general paucity of information on tidal channel invertebrate communities in the estuary, evidence of tidal channel use by both transient and marsh resident fishes, and the uncertainty of faunal responses to marsh restoration projects, we undertook this study in the northern estuary for two reasons:

1. To determine what physical and biological variables (e.g., position along the estuarine gradient, local vegetation assemblage, channel metrics, and marsh restoration age) explain spatial and temporal variations in benthic/epibenthic and neustonic invertebrate communities, and
2. To examine fish diets as functional indicators of marsh food web variation, testing for feeding differences among species, marsh locations, and seasons, as well as examining relationships between fish diets and potential environmental drivers.

METHODS

We sampled six tidal marsh sites in northern San Francisco Bay ([Figure 1A](#)) over seven quarterly sampling events: October 25–28 through November 10–11, 2003; February 13–18, June 14–19, and September 26–30, 2004; and January 8–13, March 26–31, and June 19–24, 2005. Each marsh site was located in one of three regional river systems that discharges into the northern estuary: Petaluma River (Carl's Marsh, [Figure 1B](#)), Napa River (Bull Island, Coon Island, Pond 2A, [Figure 1C](#)), and the west Delta (Sherman Lake, Browns Island, [Figure 1D](#)). Being connected to the San Francisco Bay, marsh sites broadly represent communities along the estuarine gradient of the estuary. However, the strength and seasonality of the hydraulic connections are somewhat different given the sub-hydrology of each river tributary. Macroinvertebrate and fish sampling was conducted in three separate channels in each of the six marshes. Selected channels were consistent among sampling dates. Marsh sites varied in size, geographic position (see Gewant and Bollens 2011), restoration status, elevation, salinity range, and vegetation community (Howe and Simenstad 2011). Via levee breaching, tidal access was restored to Carl's Marsh in 1994, Pond 2A in 1995, Bull Island in 1982, and Sherman Lake in 1934. Coon Island and Browns Island are ancient marshes that have been physically untouched, and thus serve as reference sites.

Environmental Variables

We collected abiotic and biotic environmental variables at region, site and channel levels ([Table 1](#)). Many of these metrics were generated as part of the larger Integrated Regional Wetlands and Monitoring (IRWM) study, and have been previously well-described (e.g., Cohen and Bollens 2008; Strahlberg et al. 2010, Gewant and Bollens 2011; Tuxen et al. 2011). Abiotic variables included both static metrics related to marsh structure or position, and dynamic metrics related to seasonal changes in flow, salinity, and temperature. A seasonal metric representing the wet and cold season versus the warm and dry season was calculated using the formula: $\sin(360/365 \times \text{Julian day})$, where November 1 was set as 0, the first day of the wet season, and each Julian day was assigned a value between 1.00 to -1.00 according to the position along the sin wave (Gewant and Bollens 2005). Channel metrics were generated using ArcView GIS software. Marsh channel edge was calculated in two ways: channel perimeter as digitized from ortho-rectified aerial photographs (2003 and 2004) and channel edge. Channel edge metrics, defined as twice the sinuous channel length, were obtained from Gewant and Bollens (2011), as was distance from each marsh to the Golden Gate, a measure of marsh position along the estuarine gradient. Other structural characteristics included areal channel density within each marsh site, channel area (m^2), marsh plain elevation, channel sinuosity, and site area.

We measured salinity and temperature using a YSI® probe at each channel immediately after we deployed the fyke net, as described below. We calculated a water column mean from surface and bottom water measurements. We obtained daily averages of Delta outflow from the Department of Water Resources DAYFLOW program (<http://www.water.ca.gov/dayflow/>). We obtained river-specific (i.e., Napa and Petaluma) outflow from U.S. Geological Survey (USGS) flow gauge data for the Napa and Petaluma rivers (<http://waterdata.usgs.gov/>). Because organism response often lags changes in abiotic environmental conditions, but the appropriate lag time during which

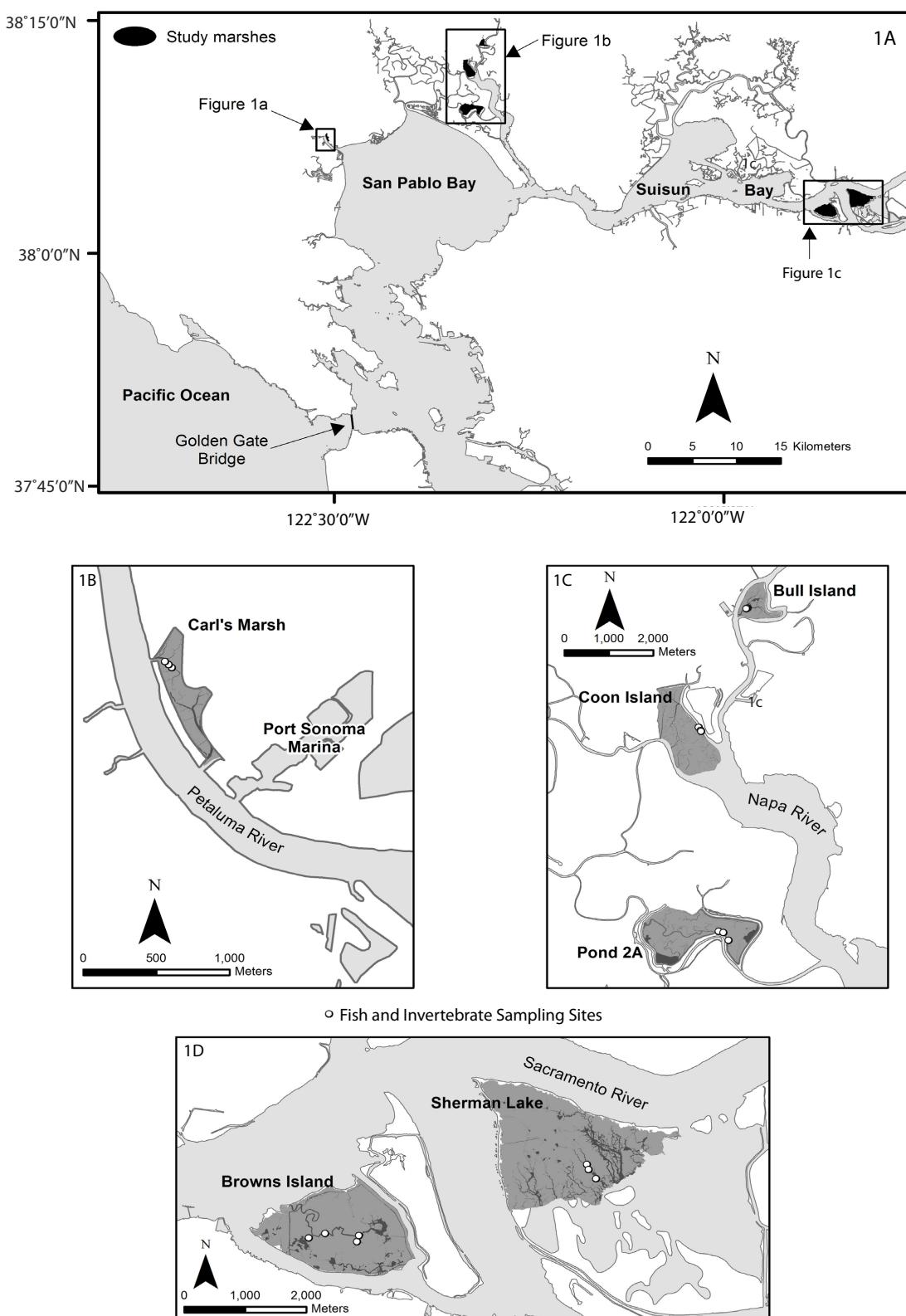


Figure 1 Marsh and channel locations of study sites in Petaluma (1B), Napa (1C), and the west Delta (1D)

Table 1 Environmental variables included in DISTLM and dbRDA analyses. Variables were collected at varying spatial and temporal scales. ED = estuary-scale metric applied (all sites), date-specific. RD = regional-scale value metric, date-specific. SD = site scale metric, date-specific. CD = channel-scale metric, date-specific. S = site scale metric, all dates. C = channel scale metric, all dates.

Type	Type	Variable	Scale	Description
Abiotic	Dynamic	Delta Flow	ED	Delta Outflow (day of sampling)
		RflowD	RD	River-specific outflow, day of sampling
		RflowW	RD	River-specific outflow, week before sampling
		RflowM	RD	River-specific outflow, month before sampling
		Salinity	CD	Averaged water column salinity of each channel
		Temperature	CD	Averaged water column temperature of each channel
		Month	ED	Month of year
		Year	ED	Year of sampling
		Season Index	ED	Continuous index contrasting Feb (cold/wet) with August (warm/dry). Varies between -1 (Aug) and 1 (Feb).
		NTI/BTI	SD	Neuston/Benthos time index. Continuous index describing time of sampling. Varies between -1 (dark to 6:00 p.m.) and 1 (light to 6:00 a.m.).
	Static	Distance to Golden Gate	S	Distance from marsh location to the Golden Gate Bridge at the SFE mouth
		Elevation	S	Mean marsh-plain elevation
		% marsh	S	% of site covered by marsh vegetation
		% water	S	% of site covered by open water
		% SAV	S	% of site covered by submerged aquatic vegetation
		ARchD	S	Areal channel density in the site
		Channel edge	C	Twice the sinuous channel length
		Channel perimeter	C	Digitized perimeter of channel
		Channel sinuosity	S	Sinuosity of channels at the site level
		Channel area	C	Area of each sampled channel (m ²)
		Site area	S	Area of each marsh
Biotic	Static	Alkali Bulrush	C	percent cover within 2m of sampling channel
		Alkali common reed	C	" "
		Bulrush	C	" "
		Cattail wetland	C	" "
		Common three-square	C	" "
		Cordgrass saline	C	" "
		Pickleweed wetland	C	" "
		Annual pickleweed	C	" "
		Grassland community	C	" "
		High marsh	C	" "
		Gumplant	C	" "
		Perennial Pepperweed	C	" "
		Himalayan blackberry	C	" "
		SAV	C	" "
		Upland	C	" "
		Bare ground	C	" "
		Water	C	" "
		vegShEI	S	Shannon Evenness Index for vegetation community
		vegShDI	S	Shannon–Weiner Diversity Index for vegetation community

organisms respond is unknown, we compiled four different flow metrics:

- Delta outflow averaged for the 14 days before sampling (inclusive of sampling date)
- river-specific flow on the day of sampling
- river-specific flow averaged over the week before sampling, and
- river-specific flow averaged over the 30 days before sampling.

We used ArcView GIS to calculate the percent cover of vegetation communities or species, as well as bare ground and open water within two meters of sampling channels. Original vegetation mapping was conducted as part of the IRWM project, and is described in detail by Strahlberg et al. (2010) and Tuxen et al. (2011). The Shannon Evenness Index and Shannon–Weiner Diversity Index were both calculated for the vegetation community at the site level.

Invertebrate Sampling

We sampled invertebrate populations associated with the benthos and epibenthos using a 5-cm diameter PVC benthic core inserted in the sediment to a depth of 10 cm, yielding a volume of 196 cm³. We refer to this group of organisms as benthic/epibenthic macroinvertebrates. We collected a total of five cores per channel (15 per site) during each sampling effort. We preserved sediments in 10% buffered formalin, dyed with rose bengal. In the lab, samples were sieved through a 500-μm sieve and identified to the lowest practical taxonomic level possible (ranging from species to order).

We sampled neuston (organisms on or immediately under the surface of the water) using a 0.41-m × 0.20-m neuston net with a 130-μm mesh net. We towed the net by hand along five 10-m transects in each channel (15 per site). We pulled tows against the current during mid-ebb tide, beginning at the channel mouth and moving upstream. We sprayed soapy water on the closed net immediately after each tow to reduce the insects' ability to fly as

we transferred them from the cod-end to sampling jars. We preserved neuston samples in 10% buffered formalin and identified to order or family level. We calculated neuston density by multiplying the length of the tow by the dimensions of the net opening.

We used data on the spatial and temporal patterns in zooplankton assemblages (S.M. Bollens, WSU, unpublished data, 2013) to inform fish selectivity analyses (see "Fish Diets"). Tidal channel zooplankton sampling coincided with benthic, epibenthic and neuston sampling.

Fish Diets

Subsampled fish were obtained from the simultaneous collections of Gewant and Bollens (2011), who used a channel fyke net set in each of three channels at each marsh site during high slack tide. Our fish data thus reflect the catch data that Gewant and Bollens (2011) report, where over 90% of fish caught were non-native; native species rarely provided robust sample sizes for informative diet analysis. We thus focus our analyses on three species: Yellowfin goby (*Acanthogobius flavimanus*), inland silversides (*Menidia beryllina*), and rainwater killifish (*Gambusia affinis*). We collected stomach contents from up to five individuals of each fish species in each channel, although sample numbers were often lower than five for a given species. Because collected fish were also used for stable isotope analysis, individuals were placed on ice in the field, and frozen. In the lab, stomach contents were dissected out and preserved in isopropanol. Prey organisms were identified to the lowest practical taxonomic level, blotted dry, and weighed to the nearest 0.0001 g. For each prey category, we calculated the frequency of occurrence (%FO), as well as the numeric (%NC) and gravimetric (%GC) contribution of each prey taxon to total prey. In addition to these individual diet metrics, we also interpreted the prey spectrum through the Index of Relative Importance (IRI; %IRI = %FC (%NC + %GC), modified from Pinkas et al. 1971).

We evaluated fish feeding selectivity by comparing the numerical (gravimetric values were not available for all potential prey) similarity among fish diet composition and prey availability as a total aggregate prey field from coincident benthic, neuston and zooplankton macroinvertebrate samples using two selectivity indices—the Ivlev Selectivity (IS) Index and the Linear Food Selection (LFS) index. We used these two indices because their values both range between +1 and -1 (negative values indicate rejection or inaccessibility of prey, zero reflects feeding in proportion to prey availability, and positive values indicate selection for a prey item). While these two indices have been found to be correlated, they have different biases, assumptions and sensitivity to sample size that allow different but comparable inferences about prey selectivity (Deudero and Morales-Nin 2001).

The Ivlev Selectivity Index (E ; Ivlev 1961) is expressed as:

$$E = \frac{r_i - p_i}{r_i + p_i} \quad (1)$$

where r_i is the relative abundance of food category i in the stomach (as a proportion or percentage of all stomach contents) and p_i is the relative abundance of the prey in the environment.

The Linear Food Selection index (L ; Strauss 1979 cited in Deudero and Morales 2001) is expressed as:

$$L = r_i - p_i \quad (2)$$

and describes the difference between the proportion of prey in the stomachs (r_i) and that available in the environment (p_i).

Statistical Analyses

We tested for differences in benthic/epibenthic and neuston community assemblages using a suite of multivariate techniques available in the PRIMER v. 6 (Clarke and Gorley 2001) and PERMANOVA, v.1 (Anderson et al. 2008) software packages. Before multivariate analysis, we combined the neuston and benthic/epibenthic sample replicates taken within

each channel by averaging across all five tows or cores to reduce sample variability at the channel level and to avoid pseudo-replication when comparing across sites. Benthic/epibenthic and neuston density data thus reflect an n of 3 at each site and date, with each sample representing one channel. We log-transformed [$\log(x+1)$] the density data for benthic/epibenthic invertebrates and neuston to reduce the influence of rare species, created similarity matrices between all site-date combinations using the Bray-Curtis distance measure, and tested for differences across dates, regions, and sites using permutational multivariate analysis of variance (PERMANOVA), a non-parametric method similar to analysis of variance that uses permutation methods to test for differences among groups (Anderson et al. 2008). For the PERMANOVA analysis, sites were nested in region (e.g., Browns Island in the west Delta) and both sites and regions were nested in sampling date. Date was treated as a random factor, while region and site were fixed factors. A separate PERMANOVA test was used to test for differences among restoring and reference marshes, with a site's restoration status nested in region, and region nested in date. Restoration status and region were treated as fixed factors, while date was treated as a random factor. Non-metric multidimensional scaling (MDS) was used to visualize differences among factors, and ANOSIM (analysis of similarity) was used to test for differences between samples collected during the day versus night. ANOSIM calculates a p -value similar to that of an ANOVA, with values of $p < 0.05$ indicating significant differences, and an R statistic scaled between -1 and 1, with the biological importance of the difference becoming greater as R approaches unity. Values greater than 0.4 are considered biologically important (Clarke and Warwick 2001). We used similarity percentages (SIMPER) to determine which taxonomic groups most contributed to dissimilarities across sites, dates, and regions. We used PRIMER's MVDISP routine to quantify multivariate dispersion (DISP) effects among sites, using a Bray-Curtis distance matrix on $\log(x+1)$ transformed invertebrate assemblage data. The routine describes differing dispersion across

groups on the basis of dissimilarity within groups (Clarke and Gorley 2001).

To relate invertebrate assemblage structure to environmental characteristics, we used PRIMER's distance-based linear modeling (DISTLM) routine and distance-based redundancy analysis (dbRDA) to analyze and visualize the amount of variation explained by a suite of environmental variables. Modeling was performed on Bray-Curtis similarity matrices based on $\log(x+1)$ transformed data and included the full suite of species identified. We used a step-wise selection procedure combined with the AIC (Akaike Information Criterion) selection criterion (measure of model quality balancing goodness of fit with model complexity) was used to select variables for inclusion in the final explanatory model. A total of 39 environmental variables was included in the full model, 17 of which describe vegetation species within two meters of sampling channels (Table 1). Environmental variables were tested for collinearity before being included in the model. Delta outflow and river-specific outflow averaged over the week before sampling were highly correlated (>0.95). However, both variables were retained in the model because river-specific outflow is equivalent to Delta outflow for the west Delta sites. As such, Delta outflow overwhelms the contribution of Napa and Petaluma "week before" outflows within the correlation matrix. We wished to retain this response time for the Napa and Petaluma rivers in the model. We wished to retain this response time for the Napa and Petaluma rivers in the model.

We square-root transformed fish diet data based on gravimetric composition before we created Bray-Curtis similarity matrices for multivariate evaluation of how environmental factors and marsh status affected variability in prey composition. We used MDS and ANOSIM routines to identify and visualize spatial and temporal differences in fish diets within and among species. We used DISTLM and dbRDA to analyze and visualize the amount of diet variation explained by a suite of environmental variables. We used step-wise regression and the AIC selection criterion to select variables for inclusion in the final model.

RESULTS

Benthic and Epibenthic Macroinvertebrates

The benthic/epibenthic macroinvertebrate community differed significantly across dates, regions, and sites (Table 2). We also observed a small, but significant effect of marsh restoration status within a date and region ($Pseudo-F = 3.4381$, $p = 0.001$). Average taxa richness was highest in Pond 2A (17.76 ± 3.04) and lowest at Sherman Lake (8.57 ± 1.28). Coon Island and Pond 2A consistently displayed the highest densities of benthic organisms, while Browns Island and Sherman Lake displayed the lowest densities (Figure 3, Appendix A). Bull Island, the most upstream site in the Napa cluster, often displayed densities similar to Browns Island in the west Delta. Community assemblage was more variable in

Table 2 PERMANOVA results of $\log(x + 1)$ transformed benthic and neuston macroinvertebrate density data. Each successive factor is nested in the previous.

	Source	df	SS	MS	Pseudo-F	P(perm)
Benthos	Date	6	18630	3104.9	5.7479	0.001
	Region(Date)	14	1.11E+05	7918.8	14.659	0.001
	Site(Region[Date])	21	39002	1857.2	3.4381	0.001
Neuston	Date	6	65192	10865	13.076	0.001
	Region(Da)	14	96431	6887.9	8.2893	0.001
	Site(Region[Da])	21	48043	2287.8	2.7533	0.001

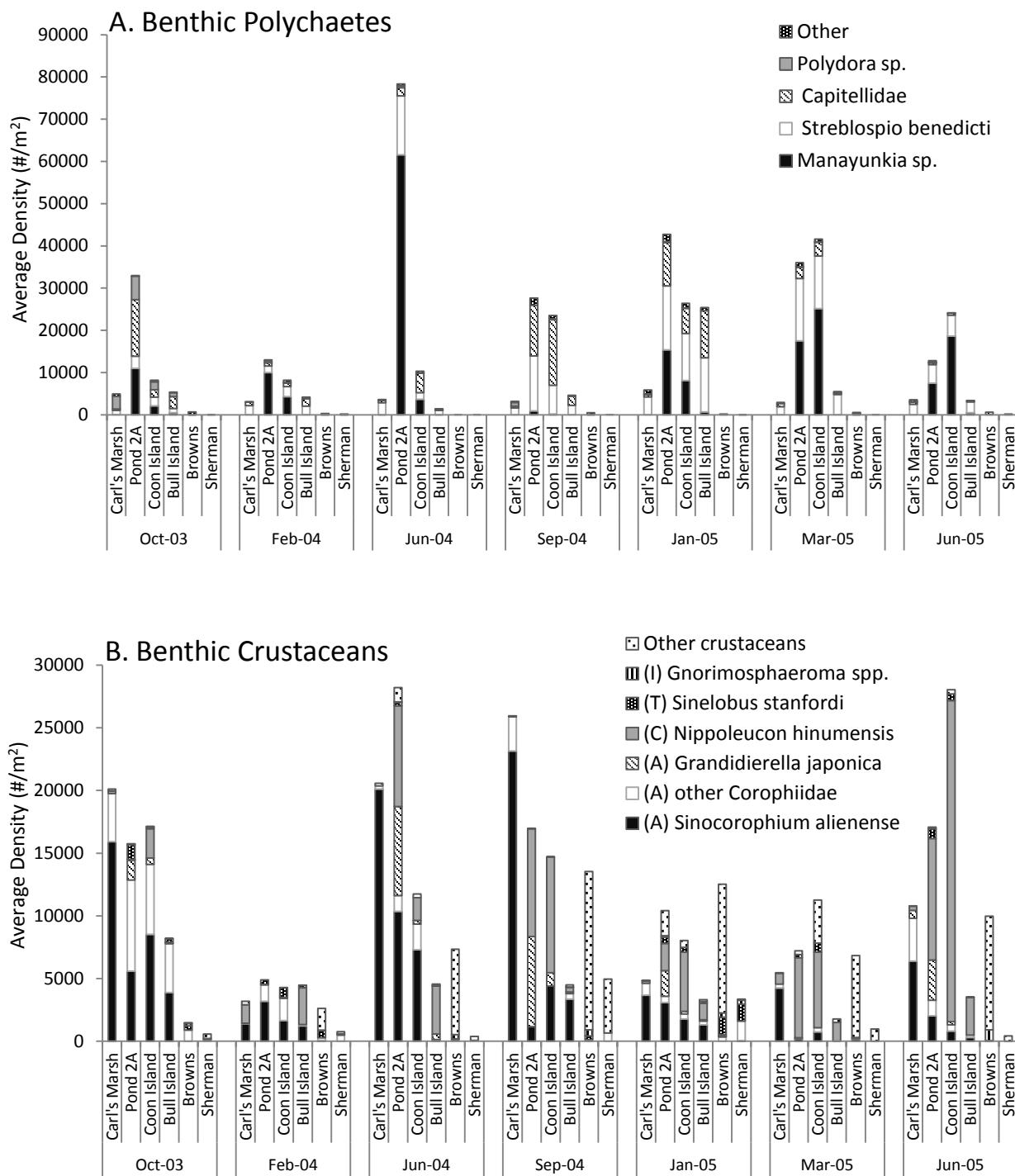


Figure 2 Average densities of benthic/epibenthic polychaetes and crustaceans collected quarterly via benthic cores in northern San Francisco Estuary interior marsh channels, 2003–2005.

the west Delta (Sherman Lake Disp = 1.43, Browns Island Disp = 1.34) and Bull Island (Disp = 1.19), and less variable at Coon Island (Disp = 0.66), Pond 2A (Disp = 0.67), and Carl's Marsh (Disp = 0.70).

With the exception of Pond 2A, the benthic community was dominated numerically by oligochaete worms, which generally comprised ~30% of the community at any one time or place. At Pond 2A, oligochaetes usually comprised ~10% of the benthic/epibenthic community. Excluding oligochaetes and nematodes, the most abundant taxa found in the benthos included polychaete worms (*Manayunkia* sp., *Streblospio benedicti*, Capitellidae, *Polydora* sp.), amphipods (*Sinocorophium alienense*, other Corophiidae, *Grandidierella japonica*), the cumacean *Nippoleucon hinumensis*, and ostracods. Ostracods were most prevalent at Browns Island. *Sinocorophium alienense* was most abundant at Carl's Marsh. *Streblospio benedicti*, *Manayunkia* sp., capitellids, *N. hinumensis*, and *G. japonica* were most abundant at Pond 2A and Coon Island (Figure 2).

The benthic/epibenthic communities in the Napa River sites were most similar to one another (Table 3); the greatest dissimilarities occurred between Sherman Lake and the more saline-influenced sites, including Coon Island (71.82% dissimilar), Pond 2A (74.53%), and Carl's Marsh (72.02%). These differences were driven mainly by the differences in abundances of *Streblospio benedicti*, *Manayunkia* sp., *N. hinumensis*, and *Sinocorophium alienense*, which were rare or absent at Sherman Lake, and ostracods, dipteran larvae, *Americorophium* spp., *Gnorimosphaeroma insulare*, and *Crangonyx* sp., which were either rare or absent in the more saline sites (Figure 4A, stress = 0.19). Strong differences also occurred between Carl's Marsh and Browns Island (70.39%), largely because of different abundances of *Sinocorophium alienense* and *Streblospio benedicti*, which were rare at Browns Island, and ostracods and chironomid larvae, which were absent in Carl's Marsh. The benthic/epibenthic community at Bull

Table 3 SIMPER results describing the percent dissimilarity between pairs of marshes for benthic macroinvertebrates and neuston. Darker shades indicate greater similarity among marshes.

	Browns Island	Sherman Lake	Bull Island	Coon Island	Pond 2A	Carl's Marsh
Benthos						
Browns Island	—	—	—	—	—	—
Sherman Lake	58.16	—	—	—	—	—
Bull Island	66.16	67.26	—	—	—	—
Coon Island	69.37	71.82	45.21	—	—	—
Pond 2A	69.98	74.53	47.86	38.36	—	—
Carl's Marsh	70.39	72.02	49.39	48.48	50.59	—
Neuston						
Browns Island	—	—	—	—	—	—
Sherman Lake	61.55	—	—	—	—	—
Bull Island	66.51	63.64	—	—	—	—
Coon Island	67.26	64.3	57.03	—	—	—
Pond 2A	65.31	61.63	53.98	54.94	—	—
Carl's Marsh	79.26	78.3	75.65	72.12	71.81	—

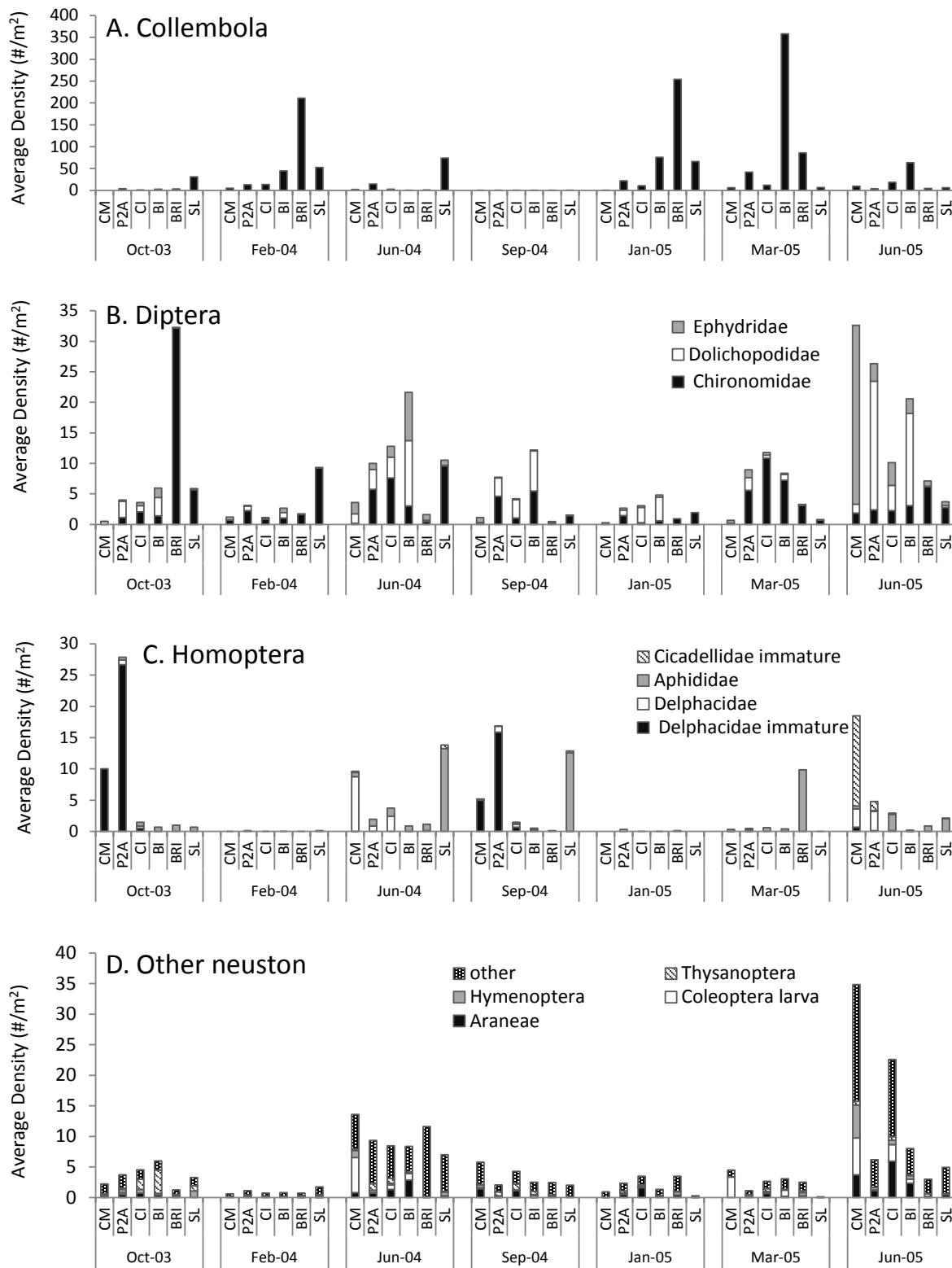
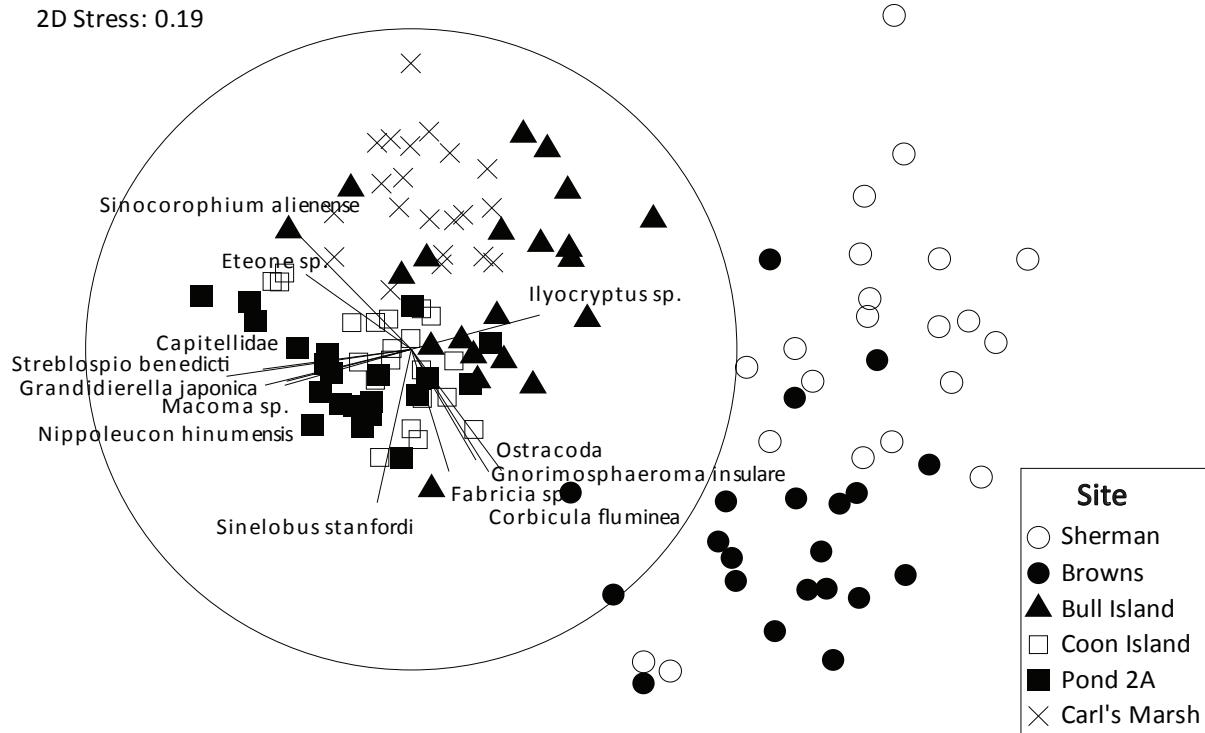


Figure 3 Neustonic invertebrates collected quarterly via surface tow nets in northern San Francisco Estuary interior marsh channels in 2003–2005. CM = Carl's Marsh, P2A = Pond 2A, CI = Coon Island, BI = Bull Island, BRI = Browns Island, SL = Sherman Lake.

A. Benthic Macroinvertebrates

2D Stress: 0.19

**B. Neuston**

2D Stress: 0.22

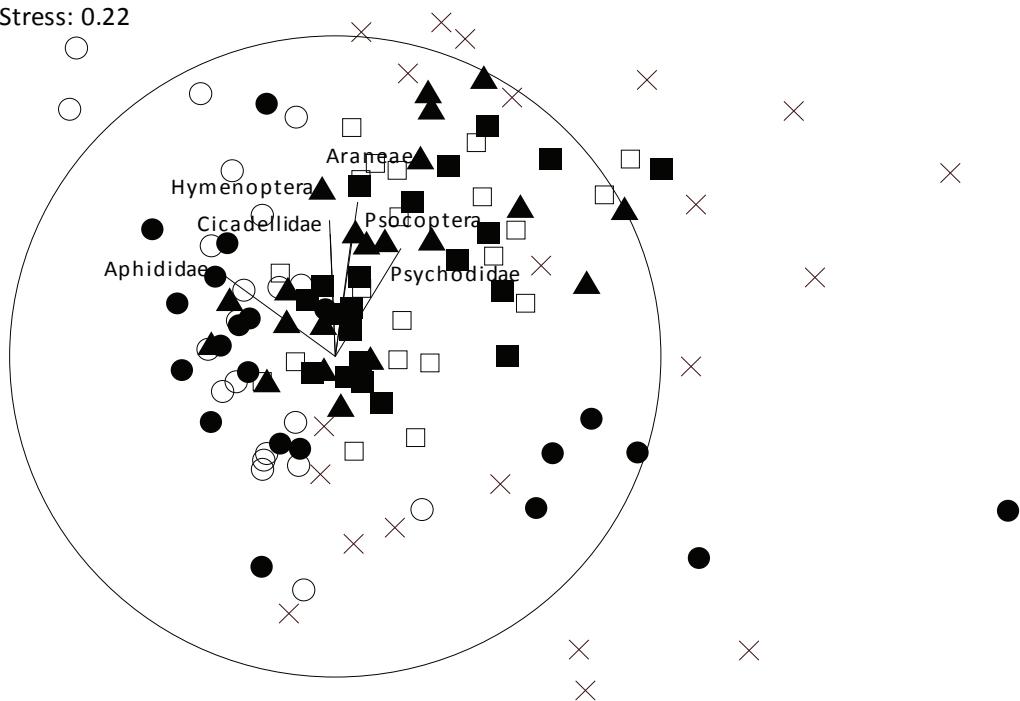


Figure 4 MDS ordination of benthic (A) and neustonic (B) community assemblages by site (based on Bray–Curtis distance measure after $\log(x + 1)$ transformation). Vectors describe invertebrate taxons with Pearson correlations >0.38 .

Island, located the furthest upstream in the Napa cluster, more resembled the west Delta sites than did the lower Napa River estuary sites, Coon Island and Pond 2A (Table 3, Appendix A¹).

Of the environmental variables collected, 35.4% of variation in benthic/epibenthic community structure was best explained by a mixture of 12 environmental variables that represent structural features within a marsh and temporally variable features that drive water chemistry and temperature shifts. Nine percent of total variation was related to the vegetative community, as well as the amount of bare ground and open water in each marsh (Figure 5A, Appendix B²). Benthic/epibenthic macroinvertebrate community variability was also explained by six environmental variables including sampling month (10.5%), seasonal temperature index (7.1%), sampling year (5.4%), freshwater flow on the day of sampling (2.4%), the time of sampling (1.1%), and channel perimeter (1.3%).

Neuston

The neuston community assemblage differed significantly across sampling dates, regions, and marsh sites (Table 2). We also observed small but significant effect of restoration status for the neuston community within a date and region ($Pseudo-F = 2.9232$, $p = 0.001$). No significant difference was observed between day and night sampling (ANOSIM $R = 0.006$). Average taxa richness peaked during June (mean = 20.7 ± 10.1), and reached a minimum during the winter (7.8 ± 1.4). Taxa richness was often highest in Pond 2A and Coon Island, and often lowest at Browns Island and Sherman Lake (Appendix C³).

¹ <https://catalyst.uw.edu/workspace/file/download/8a522155ff5645f2716bef73d3729640e73f7e42ead70b2cff9d25a69bfdaa1e?html=1&url=https://catalyst.uw.edu/workspace/file/download/8a522155ff5645f2716bef73d3729640e73f7e42ead70b2cff9d25a69bfdaa1e>

² <https://catalyst.uw.edu/workspace/file/download/8a522155ff5645f2716bef73d3729640accd868338790cc4c2f4fa29472190c3?html=1&url=https://catalyst.uw.edu/workspace/file/download/8a522155ff5645f2716bef73d3729640accd868338790cc4c2f4fa29472190c3>

³ <https://catalyst.uw.edu/workspace/file/download/8a522155ff5645f2716bef73d3729640c78d6c49393efcc0aeb44352b241ce1d?html=1&url=https://catalyst.uw.edu/workspace/file/download/8a522155ff5645f2716bef73d3729640c78d6c49393efcc0aeb44352b241ce1d>

Overall, Collembolans (springtails) were the most abundant organisms found in the neuston, followed by mites (Acari), dipteran insects (Chironomidae, Dolichopodidae, and Ephydriidae), and homopterans (Delphacidae, Aphididae, and Cicadellidae) (Appendix C). Excluding Collembola and Acari, average neuston density (number per m²) peaked during the summer and early fall (June through October), but we did not observe an emergent pattern across sites (Figure 3). Collembolan densities were variable across sites and dates, but tended to peak during the winter and early spring, a pattern opposite the remaining neustonic organisms (Figure 3). Collembolan densities were especially high during the winter in the more fluvially-influenced sites, including Browns Island, Sherman Lake, and Bull Island. Community assemblage was more variable at Browns Island (Disp = 1.2) and Carl's Marsh (Disp = 1.45), and less variable at Pond 2A (Disp = 0.77).

The neuston community split largely between the west Delta sites and the Napa and Petaluma sites. Araneae (spiders), Psocoptera (primitive hemipterans), and Psychodidae (dipteran insects) were more abundant in the Napa and Petaluma regions, whereas Aphididae (aphids), Hymenoptera (ants, bees, wasps, and sawflies), and Cicadellidae (leaf hoppers) were more abundant in the west Delta sites (Figure 4B, although the high MDS stress value affects the display of multivariate community data, obscuring the split between the west Delta and remaining sites). At Browns Island in the west Delta, 90.4% of the neuston was comprised of Collembola, Chironomidae, Acarina, Aphididae, *Rhagovelia sp.*, and hymenopterans. At Sherman Lake, 90.1% of the neuston community was characterized by Collembola, Chironomidae, and Aphididae. In the Napa sites (Bull, Coon, and Pond 2A), Collembola, Dolichopodidae, Chironomidae, Acarina, Ephydriidae, and Araneae comprised > 80% of the neuston community. In the Petaluma (Carl's Marsh), Collembolans, ephydrids, delphacids, and coleopteran larvae comprised 58% of the neuston. All other categories contributed < 5% to the overall community composition.

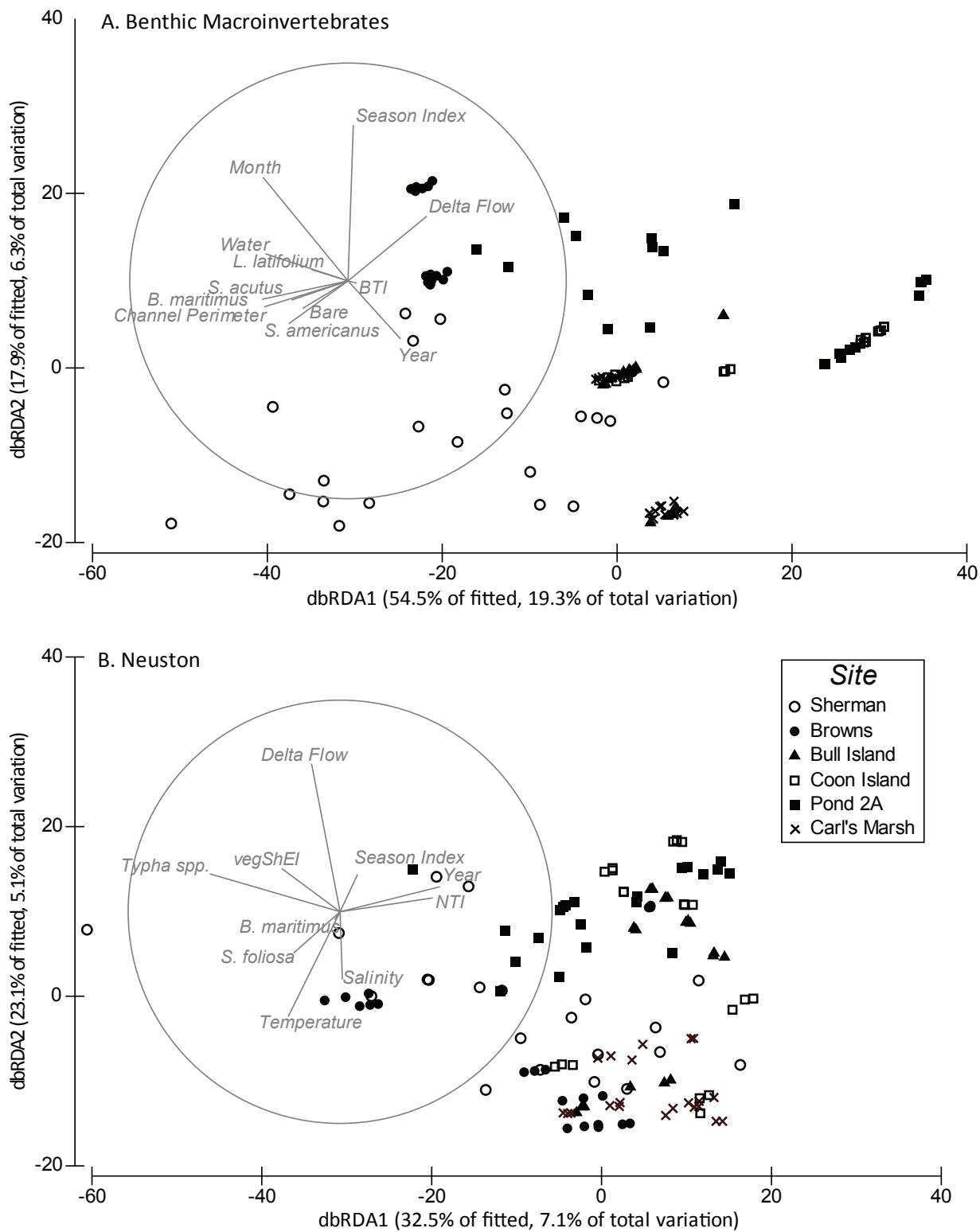


Figure 5 Distance-based RDA (dbRDA) ordination for the fitted models of benthic macroinvertebrate and neuston data (based on Bray–Curtis distance measure after $\log(x + 1)$ transformation) versus environmental variables

With respect to similarity in the community structure of neuston between sites, SIMPER analyses revealed a different structure than that observed for the benthic community. The greatest dissimilarities consistently occurred in comparisons with Carl's Marsh (> 70% dissimilar), whereas the benthic community differed most in site comparisons with Sherman Lake. Similar to the benthic community, however, the neuston communities inhabiting the Napa marshes were most similar to one another (Table 3). Furthermore, the neuston assemblage at Browns Island differed more from the Napa and Petaluma marshes than did the neuston assemblage at Sherman Lake, although not dramatically (Table 3). Located the furthest upstream in the Napa cluster, the benthic community at Bull Island showed a greater resemblance to the west Delta sites than did Coon Island and Pond 2A in the lower Napa River estuary (Table 3).

Distance-based linear models determined that 21.99% of variation in neuston community assemblage structure could be explained by 12 variables. Biological variables related to the vegetation community at each site explained 7% of variation in neuston community composition. Neuston responded to the presence of cattail wetlands (*Typha* spp., 3.1%), Pacific cordgrass (*Spartina foliosa*, 2.1%), Alkali bulrush, (*Bulboschoenus maritimus*, 1.3%), and Shannon's Evenness Index. Abiotic environmental variables governing neuston community composition comprised the remaining 15% of explained variation, including sampling month, season index, year, time of day (normalized time index, NTI), salinity, water temperature, and Delta outflow on the day of sampling (Appendix B). Taken together, these variables generally describe the hydrography and seasonal temperature shifts that underlie the sampling regions and periods. Axis 1 of the dbRDA plot explained 7.1% of total variation and was most strongly related to the presence of cattail (*Typha* spp.) wetlands; Axis 2 explained 5.1% of total variation and was most strongly related to water temperature and salinity (Figure 5B, Appendix B). Variation in the neuston community assemblage was thus explained by chang-

es in vegetation community assemblages as well as seasonal shifts in temperature and salinity.

Fish Diet Composition

Diet composition was available for eight species of fish captured in the tidal channels, but the distribution of adequate sample sizes among the study marshes allowed for analysis of only inland silversides (*Menidia beryllina*), yellowfin goby (*Acanthogobius flavimanus*), and western mosquitofish (*Gambusia affinis*); although not discussed herein, incomplete diet composition data are also available for five other species—striped bass (*Morone saxatilis*), Pacific staghorn sculpin (*Leptocottus armatus*), threespine stickleback (*Gasterosteus aculeatus*), rainwater killifish (*Lucania parva*) and tule perch (*Hysterocarpus traski*)—(Table 4, Appendices D⁴ and E⁵). These species reflect the dominant components of the fish assemblages captured between October 2003 and June 2005 in the 18 marsh channel systems of three northern estuary river regions. The three dominants also represent three different combinations of feeding preference and marsh fidelity—pelagic transient (inland silverside), surface-feeding resident (western mosquitofish), and demersal resident (yellowfin goby) (Gewant and Bollens 2011).

Inland Silversides (*Menidia beryllina*)

The overall diet composition of inland silversides was dominated by benthic/epibenthic crustaceans, including the cumacean *N. hinumensis*, and corophiid and gammarid amphipods, principally *S. alienense* and *G. japonica*, respectively (Table 5). In general, these crustaceans were either numerically (i.e., *N. hinumensis*, %NC: 25.03) or gravimetrically (i.e., *G. japonica*, %GC: 13.29) important, or both (i.e., *S. alienense*,

⁴ <https://catalyst.uw.edu/workspace/file/download/8a522155ff5645f2716bef73d3729640c331241ae636e62c337272e70d98b343?html=1&url=https://catalyst.uw.edu/workspace/file/download/8a522155ff5645f2716bef73d3729640c331241ae636e62c337272e70d98b343>

⁵ <https://catalyst.uw.edu/workspace/file/download/8a522155ff5645f2716bef73d3729640c4eb637c89380d303a91d3ec235ae07f?html=1&url=https://catalyst.uw.edu/workspace/file/download/8a522155ff5645f2716bef73d3729640c4eb637c89380d303a91d3ec235ae07f>

%NC: 19.00, %GC: 17.74) but all were represented commonly in the diet (%FO = 21% to 46%). Calanoid (primarily *E. affinis* but also incidentally *P. forbesi*) and harpacticoid copepods and adult chironomid (dipteran) flies were also numerically prominent or occurred frequently in *M. beryllina* diets, but reflected low %IRI (Table 5).

Among the known origins of the dominant inland silverside prey, all were non-indigenous macroinvertebrates (*E. affinis*, *N. hinumensis*, *G. japonica*, and *S. alienense*). However, while many likely taxa among the other common prey categories (e.g., Harpacticoida, Gammaridea, Chironomidae) were classified as unknown origin, many indigenous species are likely included therein.

Although inland silversides fed consistently on benthic/epibenthic macroinvertebrates throughout northern estuary marshes, corixid hemipteran insects occurred uniquely in the diets from Sherman Lake. *Nippoleucon hinumensis* and gammarid amphipods other than Corophiidae, that were fed on prominently in the Napa marshes, were not eaten in Sherman Lake (Table 5). Chironomidae were the only prey exhibiting spatial overlap across all the marshes.

To examine differences in inland silverside diets among different marshes, we analyzed gravimetric diet composition from September 2004 in Bull Island, Coon Island, Pond 2A, and Sherman Lake⁶. Overall, minimal site-based differences were observed during this time period, with Sherman Lake separating significantly from the Napa sites (MDS 2D stress: 0.01, Table 6). Distance-based linear modeling showed that spatial differences in inland silverside diets between the west Delta and Napa marshes was from geographic site location along the estuarine gradient (14.4% of variation), as well as the presence of the bulrush *Bulboschoenus maritimus* (6.9% of variation) (Table 6).

Silverside diets were also analyzed across seasons within Coon Island and Pond 2A. Within Coon Island,

we observed no biologically important seasonal diet differences overall ($R = 0.261$, $p = 0.005$). When examined at the pairwise level (sampling dates), differences in diets largely emerged between seasons, but not necessarily with respect to flow (Table 6, wet vs. dry seasons). In general, inland silversides from Coon Island consumed benthic amphipods and neustonic insects in all seasons (Figure 6A). DISTLM results indicated that shifts in silverside diets within Coon Island were associated with day or night sampling (9.7%), temperature (10.3%), season (7.3%), and the flow of the Napa River on the day of sampling (6.1%) (MDS stress 0.08) (Table 6). In Pond 2A, silverside diets shifted slightly across sampling dates overall ($R = 0.371$, $p = 0.001$), and biologically important differences in diets were observed between the summer and winter seasons (Table 6). DISTLM results showed that silverside diets in Pond 2A responded to season (16.3%), Napa River flow the week before sampling (7.1%), and Delta outflow (6.9%). A mixture of benthic/epibenthic amphipods, cumaceans and neustonic insects were consumed year-round (Figure 6B).

Yellowfin Goby (*Acanthogobius flavimanus*)

Similar to inland silversides, yellowfin goby fed on benthic/epibenthic crustaceans. The dominant amphipod in the diet was *S. alienense*, but other amphipods such as *Hyalella azteca* and *Ampithoe* spp., polychaetes, and the isopod *G. japonica*, were observed as well. Yellowfin goby also fed extensively (both numerically and gravimetrically) and frequently on *G. oregonensis* (Table 5). Other prey occurring frequently in the diets, but not numerically or gravimetrically prominent, were *N. hinumensis*, the mysid *N. kadiakensis* and harpacticoid copepods.

In contrast to the inland silversides, the origins of dominant yellowfin goby prey, where known, were at least 40% indigenous (*N. kadiakensis*, *G. oregonensis*) compared to non-indigenous prey taxa (*N. hinumensis*, *S. alienense*, *M. beryllina*).

Differences in yellowfin goby diet compositions were most evident during September 2004 ($R = 0.748$,

⁶ Silversides were captured in Browns Island as well, but because their stomachs were empty, they were excluded from this analysis.

Table 4 Comprehensive list of all taxa present in the diets of estuarine fishes collected quarterly by fyke netting from northern San Francisco Estuary interior marsh channels in 2003-2005.

Phylum	Class	Order	Family	Genus and species	Life history or parts	A. flavimanus n = 74	G. affinis n = 37	M. beryllina n = 114
Annelida	subclass Hirudinea				adult	X		
	subclass Oligochaeta				adult	X		
	Polychaeta				adult	X		X
			Eteone spp.		adult	X		
			Capitellidae	<i>Manayunkia aestuarina</i>	adult			
			Nereididae	<i>Streblospio benedicti</i>	adult	X		
				<i>Neanthes</i> spp.	adult	X	X	
					adult	X		
Arthropoda (subphylum Chelicerata)								
Arachnida								
	subclass Acari							
	Pycnogonida	Araneae			adult	X		X
					adult	X	X	
			Pycnogonidae		adult	X		
Arthropoda (subphylum Crustacea)								
Branchiopoda								
	suborder Cladocera		Daphniidae	<i>Daphnia</i> spp.	adult	X		X
					adult			X
					egg			X
Malacostraca								
	suborder Gammaridea							
				<i>Ampelisca abdita</i>	adult	X	X	X
				<i>Ampithoe</i> spp.	adult	X		
				<i>Eogammarus confervicolus</i>	adult			
				<i>Grandidierella japonica</i>	adult	X		X
				<i>Crangonyx</i> spp.	adult	X		
				<i>Gammarus daiberi</i>	adult	X		X
				<i>Hyalella azteca</i>	adult	X		X
			Corophiidae		adult	X	X	X
				<i>Americorophium spinicorne</i>	adult	X		
				<i>Sinocorophium alienense</i>	adult	X	X	X
			Talitridae		adult	X		
				<i>Traskorchestia traskiana</i>	adult			
				<i>Traskorchestia</i> spp.	adult	X		
			Cumacea		adult	X	X	X
				<i>Nippoleucon hinumensis</i>	adult	X		
				<i>Cumella vulgaris</i>	adult	X		X
Decapoda					megalopa			
infraorder Brachyura								
infraorder Caridea			Palaemon macrodactylus		adult			
suborder Pleocyemata					adult	X		
	Astacidae							
Isopoda (suborder Flabellifera)					juvenile	X		
				<i>Gnorimosphaeroma insulare</i>	adult	X		X
				<i>Gnorimosphaeroma oregonensis</i>	adult	X	X	
				<i>Gnorimosphaeroma</i> spp.	adult		X	X
Isopoda (suborder Oniscidea)								
				<i>Porcellio scaber</i>	adult	X		
Isopoda (suborder Valvifera)								
				<i>Idotea</i> spp.	adult			X
Mysida								
				<i>Neomysis kadiakensis</i>	juvenile-adult	X		X

Phylum	Class	Order	Family	Genus and species	Life history or parts	A. <i>flavimanus</i> n = 74	G. <i>affinis</i> n = 37	M. <i>beryllina</i> n = 114
		superorder Eucarida			larva		X	
		Tanaidacea			adult	X	X	
				<i>Pancolus californiensis</i>	adult	X		
				<i>Sinelobus stanfordi</i>	adult	X		
		Maxillopoda (subclass Copepoda)			adult			
		Calanoida		<i>Eurytemora affinis</i>	adult		X	X
				<i>Pseudodiaptomus forbesi</i>	adult		X	X
		Cyclopoida		<i>Tortanus</i> spp.	adult	X		
				<i>Hemicyclops</i> spp.	adult	X		
				<i>Halicyclops</i> spp.	adult			X
				<i>Limnoithona</i> spp.	adult			X
		Harpacticoida			adult	X	X	X
	Ostracoda				adult	X	X	
Arthropoda (subphylum Hexapoda)					adult		X	X
					larva	X		X
		Coleoptera	Heteroceridae		adult		X	X
			Noteridae		adult		X	
			Staphylinidae		adult		X	X
		Diptera			larva	X	X	X
					pupa			X
			Ceratopogonidae		larva	X		
				<i>Bezzia</i> spp.	larva	X		
			Chironomidae		larva	X		X
					pupa		X	X
					adult		X	X
		Hemiptera	Culicidae		pupa	X		
			Dolichopodidae		adult		X	
			Tipulidae		larva	X		X
					nymph	X		
			Cicadellidae		adult	X		
			Corixidae		adult	X		
			Delphacidae		adult		X	
			Veliidae		adult	X		
		Hymenoptera						
			Formicidae		adult		X	
		Trichoptera			larva	X		
Entognatha								
		Collembola			adult	X	X	
Chordata	superclass Osteichthyes				larva-juv-adult			
	Atheriniformes			<i>Menidia beryllina</i>	larva-juv-adult	X		
	Cyprinodontiformes			<i>Lucania parva</i>	adult			
	Gasterosteiformes			<i>Gasterosteus aculeatus</i>	adult			
	Perciformes			<i>Acanthogobius flavimanus</i>	juvenile			
Cnidaria	Hydrozoa				adult			
Mollusca	Bivalvia		Sphaeriidae		adult	X		
	Gastropoda				adult	X		
Other				Bivalve siphon		X		
				Unidentified egg		X		
				Fish scale		X		
				Plant matter		X		X

Table 5 Diets of *Menidia beryllina*, *Acanthogobius flavimanus*, and *Gambusia affinis* collected by fyke net in northern estuary interior marsh channels in 2003–2005. %NC = percent numerical count, %GC = percent gravimetric count, %FO = percent frequency observed, %IRI= percent index of relative importance.

Prey category	Life history and parts	Origin	Ecological category	<i>Menidia beryllina</i>				<i>Acanthogobius flavimanus</i>			
				n = 114; 21 to 88 mm TL				n = 174; 34 to 140 mm TL			
				%NC	%GC	%FO	%IRI	%NC	%GC	%FO	%IRI
Mollusca											
Bivalvia											
Sphaeriidae	adult	U	benthic–epibenthic								
Gastropoda	adult	U	benthic–epibenthic								
Annelida	adult										
Polychaeta	adult	U	benthic–epibenthic	0.06	0.09	0.88	0.00	1.18	0.37	8.11	0.45
<i>Eteone</i> spp.	adult	U	benthic–epibenthic					0.20	0.17	1.35	0.02
<i>Manayunkia aestuarina</i>	adult	I	benthic–epibenthic								
<i>Streblospio benedicti</i>	adult	I	benthic–epibenthic					0.78	0.02	1.35	0.04
Capitellidae	adult	U	benthic–epibenthic					3.33	0.09	1.35	0.17
Nereididae	adult	U	benthic–epibenthic					2.64	4.72	12.16	3.23
<i>Neanthes</i> spp.	adult	U	benthic–epibenthic					0.10	0.80	1.35	0.04
Oligochaeta	adult	U	benthic–epibenthic					0.10	0.12	1.35	0.01
Hirundinea	adult	U	benthic–epibenthic					0.39	7.15	1.35	0.37
Araneae	adult	U	terrestrial	0.06	0.09	0.88	0.00	0.10	0.03	1.35	0.01
Arthropoda											
Acari	adult	U	benthic–epibenthic					0.20	0.01	2.70	0.02
Crustacea	adult	U	unknown	0.12	0.31	1.75	0.02	0.88	6.55	8.11	2.17
Pycnogonidae	adult	U	benthic–epibenthic								
Ostracoda	adult	U	epibenthic–epibenthic					1.67	0.04	2.70	0.17
Cladocera	adult	U		0.12	0.13	0.88	0.01				
<i>Daphnia</i> spp..	adult	U	planktonic–nektonic	2.14	1.63	9.65	0.90				
	egg	U									
Copepoda	adult	U	planktonic–nektonic	0.17	0.40	1.75	0.02				
Calanoida											
<i>Eurytemora affinis</i>				14.43	2.33	16.67	6.89				
<i>Pseudodiaptomus forbesi</i>				3.13	0.31	2.63	0.22				
<i>Tortanus</i> spp.								0.10	0.01	1.35	0.01
Cyclopoida											
<i>Hemicyclops</i> spp.	adult	U	planktonic–nektonic					0.29	0.01	1.35	0.01
<i>Halicyclops</i> spp.	adult	U	planktonic–nektonic	0.06	0.04	0.88	0.00				
<i>Limnoithona</i> spp.	adult	N	planktonic–nektonic	0.12	0.09	7.15	0.01				
Harpacticoida	adult	U	benthic–epibenthic	16.98	0.53	4.39	1.89	5.48	0.18	14.86	5.04
Mysidacea											
<i>Neomysis kadiakensis</i>	juvenile-adult	I	planktonic–nektonic	0.06	0.04	0.88	0.00	4.31	5.11	14.86	5.04
Cumacea											

Prey category	Life history and parts	Origin	Ecological category	<i>Menidia beryllina</i>				<i>Acanthogobius flavimanus</i>			
				n = 114; 21 to 88 mm TL				n = 174; 34 to 140 mm TL			
				%NC	%GC	%FO	%IRI	%NC	%GC	%FO	%IRI
<i>Nippoleucon hinumensis</i>	adult	N	benthic–epibenthic	25.03	14.74	45.61	44.73	7.64	0.52	13.51	3.97
<i>Cumella vulgaris</i>	adult	I	benthic–epibenthic	0.17	0.13	1.75	0.01				
Tanaidacea	adult	U	benthic–epibenthic					1.47	0.07	4.05	0.22
Tanaidae	adult	U	benthic–epibenthic					0.20	0.04	2.70	0.02
<i>Pancolus californiensis</i>	adult	I	benthic–epibenthic					0.29	0.01	1.35	0.02
<i>Sinelobus stanfordi</i>	adult	N	benthic–epibenthic					1.18	0.12	4.05	0.19
Isopoda											
<i>Gnorimosphaeroma insulare</i>	adult	I	benthic–epibenthic	0.23	0.35	1.75	0.03	0.98	0.23	1.35	0.06
<i>Gnorimosphaeroma oregonensis</i>	adult	I	benthic–epibenthic					20.67	19.50	22.97	33.23
<i>Gnorimosphaeroma</i> spp.	adult	I	benthic–epibenthic	0.12	0.09	1.75	0.01				
<i>Porcellio scaber</i>	adult	I	benthic–epibenthic					0.10	0.63	1.35	0.04
<i>Idotea</i> spp.	adult	U	benthic–epibenthic	0.06	0.04	0.88	0.00				
Amphipoda	adult	U	benthic–epibenthic	0.52	1.10	4.39	0.18	1.67	0.44	2.70	0.20
Gammaridea	adult	U	benthic–epibenthic	2.84	20.20	25.44	14.45	1.76	15.95	32.43	26.52
<i>Ampithoe</i> spp.	adult	U	benthic–epibenthic					4.90	3.47	2.70	0.81
<i>Grandidierella japonica</i>	adult	N	benthic–epibenthic	2.90	13.29	4.39	1.75	1.76	1.14	1.35	0.14
<i>Hyalella azteca</i>	adult	U	benthic–epibenthic					0.10	0.01	1.35	0.01
<i>Gammarus daiberi</i>	adult	N	benthic–epibenthic	0.06	0.97	0.88	0.02	0.49	0.55	2.70	0.10
<i>Hyalella azteca</i>	adult	U	benthic–epibenthic	0.87	4.36	5.26	0.68	3.04	11.90	2.70	1.45
Corophiidae	adult	U	benthic–epibenthic	3.53	7.13	23.68	6.23	1.67	0.44	9.46	0.72
<i>Americorophium spinicorne</i>	adult	I	benthic–epibenthic					0.59	0.44	4.05	0.15
<i>Sinocorophium alienense</i>	adult	N	benthic–epibenthic	19.00	17.74	21.05	19.07	12.24	2.98	22.97	12.60
<i>Traskorchestia</i> spp.	adult	U	benthic–epibenthic					2.06	0.89	1.35	0.14
Eucarida	larva	U	planktonic–nektonic	0.06	0.04	0.88	0.00				
Decapoda	megalopa	U	planktonic–nektonic	0.06	0.04	0.88	0.00				
Caridea		U									
<i>Palaemon macrodactylus</i>	adult	N	benthic–epibenthic					0.10	0.75	1.35	0.04
Brachyura	adult	U									
Astacidae	juvenile	U	benthic–epibenthic					0.10	0.15	1.35	0.01
Hexapoda (Insecta)	larva	U	benthic–epibenthic	0.29	0.66	4.39	0.10	0.10	0.01	1.35	0.01
Coleoptera	larva	U	benthic–epibenthic	0.06	0.04	0.88	0.00				
	adult	U	terrestrial	0.06	0.13	0.88	0.00				
Noteridae	adult	U	terrestrial	0.41	2.82	2.63	0.21				
Diptera	Larva	U	benthic–epibenthic	0.12	0.09	1.75	0.01	1.76	0.26	8.11	0.59
	pupa	U	benthic–epibenthic	0.23	0.62	2.63	0.06				
Ceratopogonidae	larva	U						0.10	0.01	1.35	0.01
<i>Bezzia</i> spp.	larva	U	benthic–epibenthic					0.29	0.01	1.35	0.01
Chironomidae	larva	U	benthic–epibenthic	0.41	0.26	2.63	0.04	0.69	0.38	2.70	0.10

Prey category	Life history and parts	Origin	Ecological category	<i>Menidia beryllina</i>				<i>Acanthogobius flavimanus</i>			
				n = 114; 21 to 88 mm TL				n = 174; 34 to 140 mm TL			
				%NC	%GC	%FO	%IRI	%NC	%GC	%FO	%IRI
	pupa	U	benthic–epibenthic	1.22	1.23	8.77	0.53				
Chironomidae	adult	U	terrestrial	1.68	1.58	11.40	0.92				
Culicidae	pupa	U	benthic–epibenthic					0.10	0.01	1.35	0.01
Dolichopodidae	adult	U	terrestrial	0.06	0.31	0.88	0.01				
Tipulidae	Larva	U	benthic–epibenthic	0.12	0.09	0.88	0.00	0.10	0.04	1.35	0.01
Corixidae	adult	U	terrestrial	0.70	3.87	6.14	0.69	0.78	0.56	6.76	0.33
Delphacidae	adult	U	terrestrial	0.35	0.75	2.63	0.07				
Veliidae	adult	U	terrestrial					0.10	0.12	1.35	0.01
Formicidae	adult	U	terrestrial	0.12	0.09	0.88	0.00				
Collembola	adult	U	terrestrial	0.93	0.26	1.75	0.05				
Chordata		U									
Osteichthyes	larva-juv-adult	U	planktonic–nektonic								
<i>Menidia beryllina</i>	larva-juv-adult	N	planktonic–nektonic					0.29	10.84	4.05	1.63
MISCELLANEOUS		U									
Bivalve siphon		U	benthic–epibenthic					0.88	0.50	5.41	0.27
Unidentified egg		U	unknown					0.10	0.13	1.35	0.01
Fish scale		U	planktonic–nektonic					1.57	0.18	6.76	0.43
Plant matter		U	unknown	0.41	0.97	5.26	0.18	0.59	0.99	8.11	0.46

Prey Category	Life History and Parts	Origin	Ecological Category	<i>Gambusia affinis</i>			
				n=37; 19-44 mm TL			
				%NC	%GC	%FO	%IRI
Mollusca							
Bivalvia							
Sphaeriidae	adult	U	benthic–epibenthic	0.43	0.44	5.41	0.18
Gastropoda	adult	U	benthic–epibenthic	0.21	0.66	2.70	0.09
Arthropoda							
Acari	adult	U	benthic–epibenthic	0.21	0.22	2.70	0.04
Crustacea	adult	U	unknown	0.85	3.76	10.81	1.89
Pycnogonidae	adult	U	benthic–epibenthic	1.49	1.11	5.41	0.53
Ostracoda	adult	U	epibenthic–epibenthic	0.85	0.44	5.41	0.26
Copepoda		U	planktonic–nektonic				
Calanoida		U	planktonic–nektonic				
<i>Eurytemora affinis</i>		N	planktonic–nektonic	4.68	0.88	5.41	1.14
<i>Pseudodiaptomus forbesi</i>		N	planktonic–nektonic	0.21	0.22	2.70	0.04
Harpacticoida	adult	U	benthic–epibenthic	51.28	0.44	5.41	10.57
Cumacea							
<i>Nippoleucon hinumensis</i>	adult	N	benthic–epibenthic	0.21	0.44	2.70	0.07
Tanaidacea	adult	U	benthic–epibenthic	0.21	0.22	2.70	0.04

Prey Category	Life History and Parts	Origin	Ecological Category	<i>Gambusia affinis</i>			
				n=37; 19-44 mm TL			
				%NC	%GC	%FO	%IRI
Isopoda							
<i>Gnorimosphaeroma insulare</i>	adult	I	benthic–epibenthic	6.17	38.27	10.81	18.17
<i>Gnorimosphaeroma oregonensis</i>	adult	I	benthic–epibenthic	14.26	20.58	35.14	46.28
<i>Gnorimosphaeroma</i> spp.	adult	I	benthic–epibenthic	0.21	0.66	2.70	0.09
Amphipoda							
Gammaridea	adult	U	benthic–epibenthic	0.85	1.55	8.11	0.74
Corophiidae	adult	U	benthic–epibenthic				
<i>Americorophium spinicorne</i>	adult	I	benthic–epibenthic	1.49	2.43	13.51	2.00
<i>Sinacorophium alienense</i>	adult	N	benthic–epibenthic	4.04	12.17	10.81	6.63
Talitridae	adult	U	benthic–epibenthic	0.21	0.22	2.70	0.04
<i>Traskorchestia traskiana</i>	adult	I	benthic–epibenthic	0.85	0.88	2.70	0.18
Hexapoda (Insecta)	larva	U	benthic–epibenthic				
	adult	U	terrestrial	0.85	0.44	5.41	0.26
Coleoptera	adult	U	terrestrial	0.21	0.22	2.70	0.04
Noteridae	adult	U	terrestrial	1.06	1.99	8.11	0.94
Staphylinidae	adult	U	terrestrial	0.21	1.33	2.70	0.16
Diptera	larva	U	benthic–epibenthic	1.06	0.66	5.41	0.35
Chironomidae	larva	U	benthic–epibenthic				
	pupa	U	benthic–epibenthic	0.43	0.66	2.70	0.11
	adult	U	terrestrial	2.98	4.87	18.92	5.61
Hemiptera	nymph	U	terrestrial	0.21	0.22	2.70	0.04
Cicadellidae	adult	U	terrestrial	0.21	1.33	2.70	0.16
Trichoptera	larva	U	benthic–epibenthic	0.21	0.22	2.70	0.04
Collembola	adult	U	terrestrial	2.98	2.21	16.22	3.18
Miscellaneous							
Unidentified egg	unknown	U	benthic–epibenthic	0.85	0.22	2.70	0.11

Table 6 ANOSIM results (left side of table) of square-root transformed gravimetric fish diet composition. Tests were run for seasonal and spatial shifts. DISTLM results (right side of table) describe the significant environmental variables driving differences in fish diets among sites or dates. BI = Bull Island, CI = Coon Island, BR = Brown's Island, P2A = Pond 2A, SH = Sherman Lake.

ANOSIM Results						DISTLM Results				
Fish species	Test	Date/Site	R	p	Wet/Dry	Env. Var	Pseudo-F	P	Prop.	Cumul.
<i>Menidia beryllina</i>										
Season										
Coon Island		0.261	0.005			Diurnal	2.793	0.009	0.097	0.097
	Feb–Jan	0.203	0.079		ww	Temperature	3.220	0.002	0.103	0.200
	Feb–Jun05	0.278	0.086		ww	Season Index	2.404	0.028	0.073	0.273
	Feb–Mar	0.571	0.067		ww	Napa R. Flow–Day of sampling	2.096	0.042	0.061	0.334
	Feb–Oct	0.161	0.286		wd					
	Feb–Sept	0.098	0.229		wd					
	Jan–Jun05	0.841	0.018	*	ww					
	Jan–Mar	1.000	0.048	*	ww					
	Jan–Oct	0.794	0.080		wd					
	Jan–Sept	0.006	0.387		wd					
	Jun05–Mar	0.750	0.100		ww					
	Jun05–Oct	0.611	0.029	*	wd					
	Jun05–Sept	0.179	0.150		wd					
	Mar–Oct	0.714	0.067		wd					
	Mar–Sept	-0.036	0.436		wd					
	Oct–Sept	0.331	0.013	*	dd					
Pond 2A		0.371	0.001	*		Season Index	6.988	0.001	0.163	0.163
	Jan–Jun	0.655	0.003	*	wd	Napa R. flow–Week before	3.254	0.005	0.071	0.234
	Jan–Jun05	0.392	0.008	*	ww	Delta Outflow	3.339	0.007	0.069	0.302
	Jan–Mar	-0.020	0.516		ww					
	Jan–Oct	0.168	0.092		wd					
	Jan–Sept	0.607	0.005	*	wd					
	Jun–Jun05	0.351	0.020	*	dw					
	Jun–Mar	0.595	0.003	*	dw					
	Jun–Oct	0.367	0.006	*	dw					
	Jun–Sept	0.345	0.011	*	dd					
	Jun05–Mar	0.084	0.294		ww					
	Jun05–Oct	0.220	0.045	*	wd					
	Jun05–Sept	0.273	0.044	*	wd					
	Mar–Oct	0.228	0.056		wd					
	Mar–Sept	0.582	0.001	*	wd					
	Oct–Sept	0.395	0.002	*	wd					
Spatial										
BI, CI, P2A, SH (Sept 2004)		0.201	0.001			Distance to Golden Gate	5.206	0.001	0.144	0.144
	BI–CI	0.018	0.318			<i>Bulboschoenus maritimus</i>	2.542	0.020	0.069	0.211
	CI–P2A	0.066	0.129							
	BI–SH	0.370	0.005	*						
	CI–P2A	0.158	0.046							
	CI–SH	0.323	0.003	*						
	P2A–SH	0.498	0.003	*						

ANOSIM Results						DISTLM Results				
Fish species	Test	Date/Site	R	p	Wet/Dry	Env. Var	Pseudo-F	P	Prop.	Cumul.
<i>Acanthogobius flavimanus</i>										
Spatial										
BI, CI, P2A, BR (June 2004)		0.133	0.001			<i>Bulboschoenus maritimus</i>	3.466	0.002	0.093	0.093
BR-BI		0.602	0.001	*		Temperature	2.126	0.031	0.055	0.147
BR-CI		0.533	0.001	*						
BR-P2A		0.036	0.587							
BI-CI		0.230	0.021							
BI-P2A		0.036	0.314							
CI-P2A		0.103	0.053							
Spatial										
BI, CI, P2A, BR (Sept 2004)		0.748	0.001	*		Channel area	4.076	0.001	0.239	0.239
BR-BI		0.981	0.008	*		Veg. Shannon Evenness Index	3.593	0.004	0.175	0.414
BR-CI		0.723	0.018	*		Site area	3.458	0.003	0.140	0.554
BR-P2A		0.851	0.018	*						
BI-CI		0.741	0.029	*						
BI-P2A		0.593	0.029	*						
CI-P2A		0.444	0.100							
<i>Gambusia affinis</i>										
Season										
Browns Island		0.433	0.001			Delta Flow—Week before	6.663	0.001	0.250	0.250
Oct–Jun		0.438	0.016	*	dd	Delta Flow—Day of	2.275	0.010	0.080	0.330
Oct–Sept		-0.069	0.683		dd	Delta Flow—Month before	2.088	0.015	0.070	0.340
Oct–Jan		0.639	0.029	*	dw					
Oct–Mar		0.541	0.024	*	dw					
Jun–Sept		0.304	0.024	*	dd					
Jun–Jan		0.615	0.018	*	dw					
Jun–Mar		0.514	0.008	*	dw					
Sept–Jan		0.754	0.018	*	dw					
Sept–Mar		0.554	0.008	*	dw					
Jan–Mar		0.231	0.196		ww					

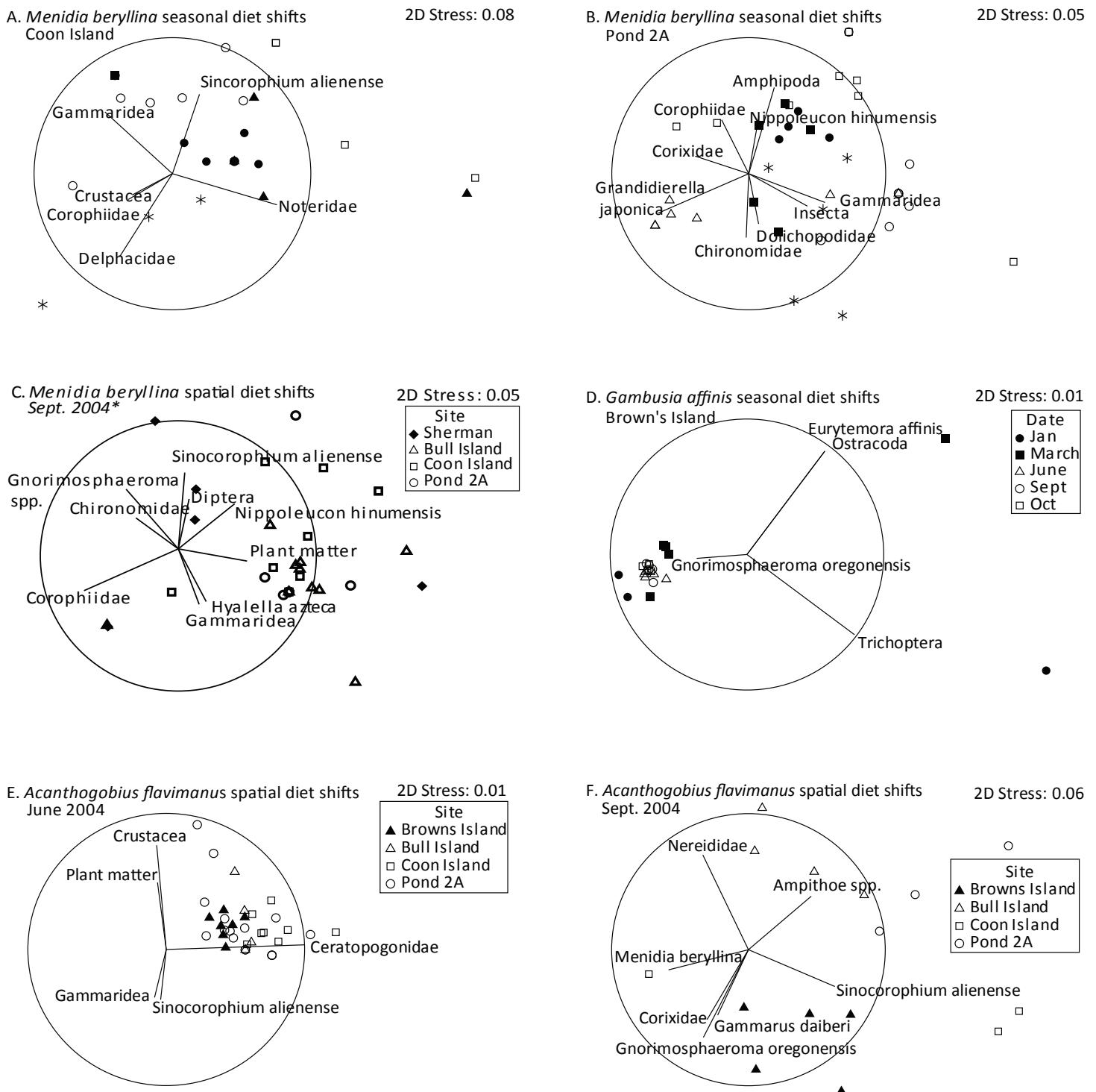


Figure 6 MDS ordination of gravimetric fish diet data (based on Bray–Curtis distance after square-root transformation). Vectors describe invertebrate prey taxons with the following Pearson correlations: (A) >0.3, (B) >0.3, (C) >0.3, (D) >0.2, (E) >0.35, (F) >0.5.

$p = 0.001$), but not during June 2004 ($R = 0.133$, $p = 0.01$) (Figures 6E, 6F; Table 6). In September, biologically meaningful diet differences were observed between all site pairs, which included Browns Island, Bull Island, Coon Island, and Pond 2A, with the exception of Coon Island and Pond 2A ($R = 0.444$, $p = 0.10$). In September, channel area (23.9%), Shannon's Evenness Index for vegetation (17.5%), and marsh area (14.0%) explained a total of 55.4% of diet variability across sites. In June, only 14.7% of diet variation among sites was explained by a combination of temperature and the presence of *Bulboschoenus maritimus* (Table 6). Yellowfin goby inhabiting Browns Island consumed *G. oregonensis*, *H. azteca*, other gammarid amphipods, and corixids. At Bull Island, gobies fed largely on nereid polychaetes and gammarid amphipods. At Coon Island, gobies largely fed on *S. alienense*. At Pond 2A, gobies mostly fed on *Ampithoe sp.* and gammarid amphipods. In June, many diet items that were previously consumed at only one or a few sites, were consumed across most sites, such as *G. oregonensis*.

Western Mosquitofish (*Gambusia affinis*)

Western mosquitofish fed almost exclusively on epibenthic harpacticoid copepods, isopods (both *G. insulare* and *G. oregonensis*) and corophiid amphipods (*A. spinicorne*, *S. alienense*), which among these taxa alone accounted for 77.5% NC, 74.8% GC, 83.8% IRI and between 5% to 35% FO (Table 5). Although harpacticoid copepods dominated the numerical composition, isopods dominated the gravimetric composition and were the most commonly represented prey in their diets. None of these *G. affinis* prey of known origins were non-indigenous, while three (*G. insulare*, *G. oregonensis*, *A. spinicorne*) were confirmed indigenous.

Gambusia affinis diets at Browns Island showed strong seasonal differences ($R = 0.433$, $p = 0.001$), largely because of significant diet shifts between high- and low-flow periods (Table 5). Delta flow metrics, including flow on the day of, the week before, and the month before sampling combined to explain

34% of the observed variability in diet composition (Table 6). During lower river flow, *G. affinis* diets were mainly composed of *G. oregonensis* and *A. spinicorne*. Less important diet items included dipteran larvae, chironomid pupae, harpacticoid copepods, Collembolans and *Noteridae*. During high river flows, *G. affinis* consumed larger proportions of chironomid adults, *G. insulare*, and *E. affinis*. Other diet items include insects and Corophiidae.

Other Notable Prey Taxa

Other macroinvertebrates appearing uniquely in the other fish diets included: polychaete annelids, *Neanthes sp.* (Staghorn sculpin, *L. armatus*); tanaids, including *Pancolus californiensis* (Rainwater killifish, *L. parva*); chironomid pupa (Three-spine stickleback, *G. aculeatus*); and, bivalve siphons and plant matter (Striped bass, *M. saxatilis*) (Appendix D). None of these prey are known to be non-indigenous.

Interspecific Diet Similarity

Finally, we observed small, but significant differences in the gravimetric composition of diets among species when nested by site and date (Pseudo-F = 3.9887, $p = 0.001$). However, pairwise tests between species within a site and date revealed no generalized pattern that governed when or where significant differences in diet occurred. Within a site, significant differences among pairwise diet comparisons showed no consistent association with season or river flow.

Prey Selection

Prey selection generally mirrored the prominent prey composing the three fishes' diet compositions (Figures 7–10). Epibenthic crustaceans were broadly selected for, and neustonic insects were often selected against, within the available prey field. The consistency in selection for *N. hinumensis*, Gammaridea, Corophiidae and *S. alienense* among sites and dates was evident for both inland silversides and bay goby (Figures 7–9); Gammaridea were also selected for by mosquitofish; the isopod *G. oregonensis* was a more

A. Coon Island

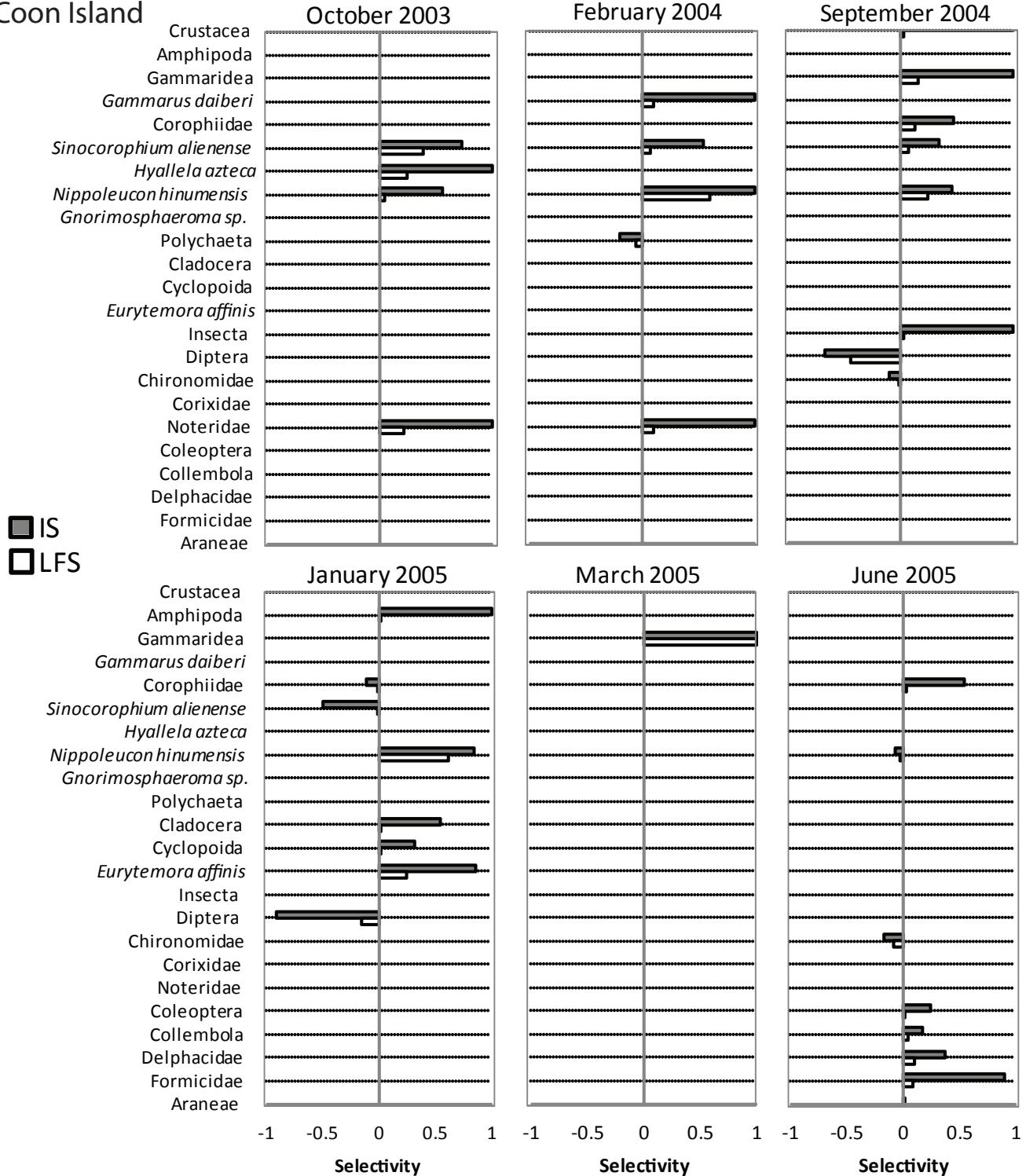


Figure 7A Seasonal differences in *Menidia beryllina* diet selectivity at Coon Island from October 2003 through June 2005, as calculated by the Ivelv Selectivity Index (IS) and the Linear Food Selection Index (LFS)

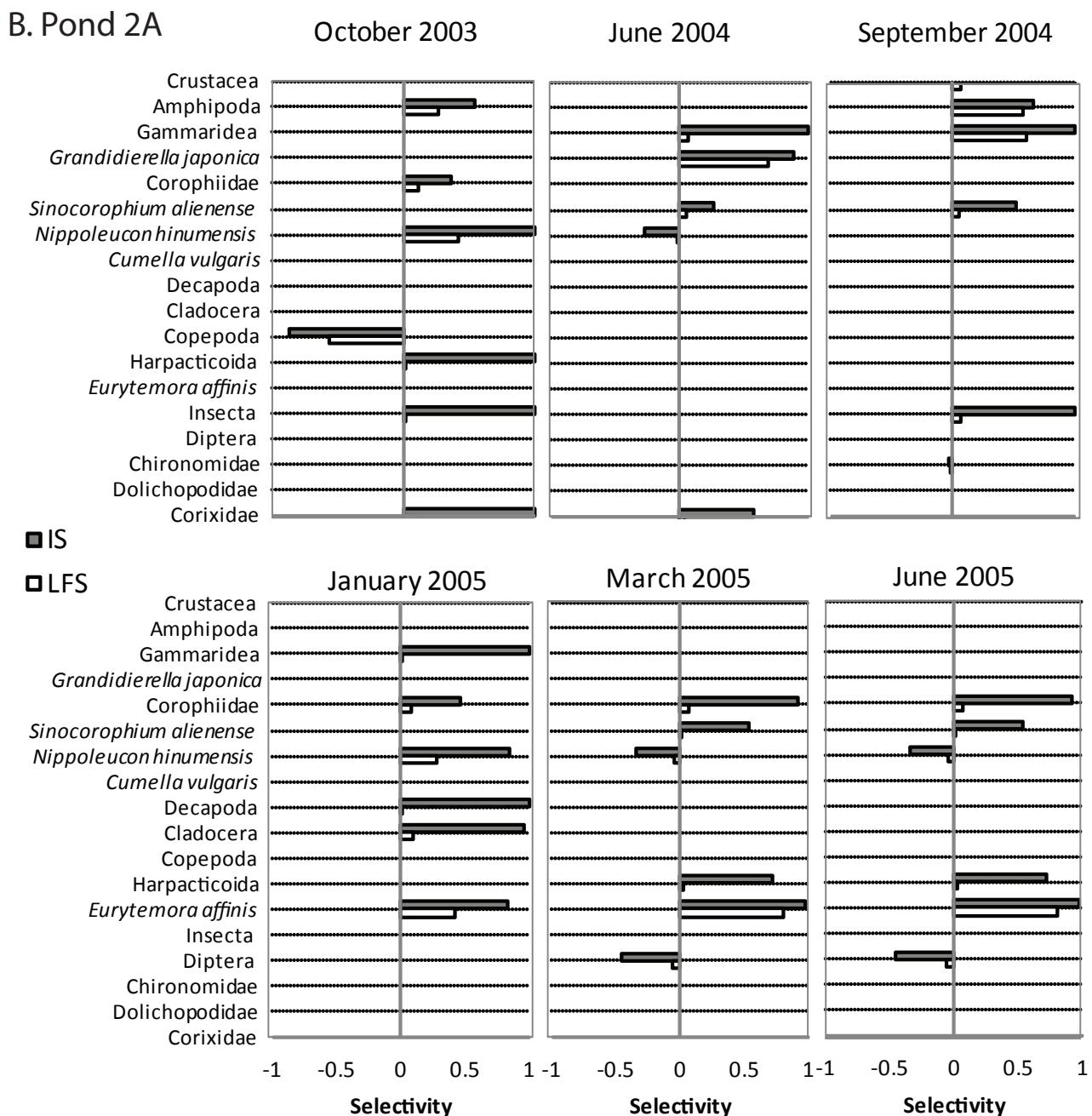


Figure 7B Seasonal differences in *Menidia beryllina* diet selectivity at Pond 2A from October 2003 through June 2005, as calculated by the Ivlev Selectivity Index (IS) and the Linear Food Selection Index (LFS)

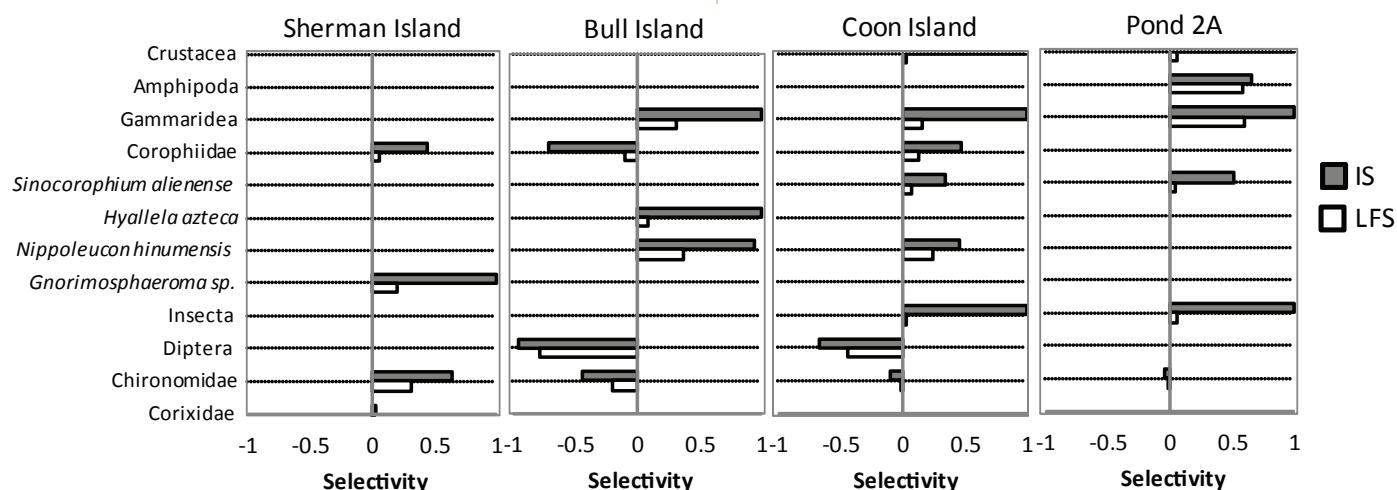


Figure 8 *Menidia beryllina* diet selectivity (IS = Ivlev Selectivity Index, LFS = Linear Food Selectivity Index) across sites in September 2004

uniquely selected prey (Figure 10). Most insect taxa within the neuston were not strongly incorporated into diets, particularly dipterans and chironomids by all three species; notable exceptions included inland silversides' selection for chironomids and corixids in Pond 2A in June 2005 and common preference for diverse neustonic insects at Coon Island by both inland silversides and yellowfin goby in the same month.

Although the LFS Index typically characterized lower scales of prey selection or avoidance than IS, coincidentally high values of both indices were noteworthy in many instances, suggesting particularly strong confidence in selection for these prey items. For instance, while many of the LFS and IS comparisons for inland silverside prey selection among the available prey field indicated LFS to be $<30\%$ of IS, it was typically $>50\%$ positive selection for *N. hinumensis* and *E. affinis*, and similarly high avoidance for chironomids and other insects. Selectivity by yellowfin goby for most prey taxa appeared weak (LFS/IS <0.3), except for *G. oregonensis* at Browns Island, *S. alienense* at Bull and Coon islands, and *Ampithoe* spp. at Pond 2A (9/04); strongly avoided prey included oligochaetes at Bull Island (9/04) and polychaetes at Pond 2A. Notable examples of

strong selection by western mosquitofish on prey at Browns Island was positive selection for *G. oregonensis* (10/03, 6/04) and harpacticoid copepods (9/04), and avoidance of dipteran insects (10/03) and Collembolans (3/05).

DISCUSSION

We found that benthic/epibenthic macroinvertebrates and neuston of tidal channels in both natural and restoring marshes of the northern estuary predominantly reflect variability in environmental variables related to seasonal changes, such as temperature, freshwater flow, and salinity, as well as to those related to marsh structure, such as the vegetation community and channel edge or perimeter. The greatest variation in abundance in our study occurred seasonally for neuston, and spatially for benthos/epibenthos, suggesting that each community responds to a different suite of environmental drivers. Interestingly, we observed minimal differences in benthic/epibenthic and neustonic invertebrate communities for marsh restoration status or age. Our data support previous work showing that restored marsh macroinvertebrate communities usually transform from a low-diversity assemblage of opportunistic colonizing species to one resembling reference conditions

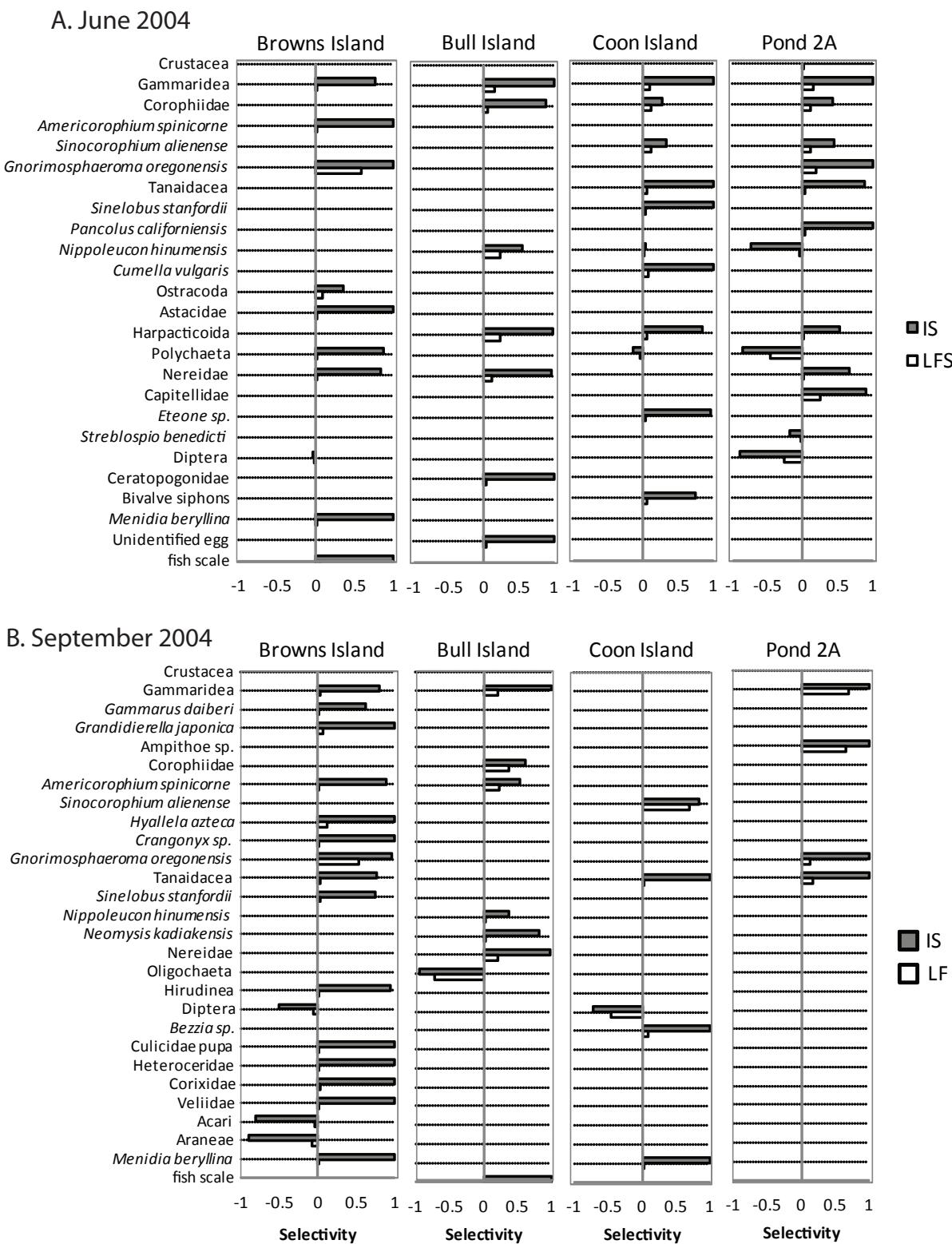


Figure 9 *Acanthogobius flavimanus* diet selectivity (IS = Ivlev Selectivity Index, LFS = Linear Food Selectivity Index) across marsh sites in (A) June 2004 and (B) September 2004

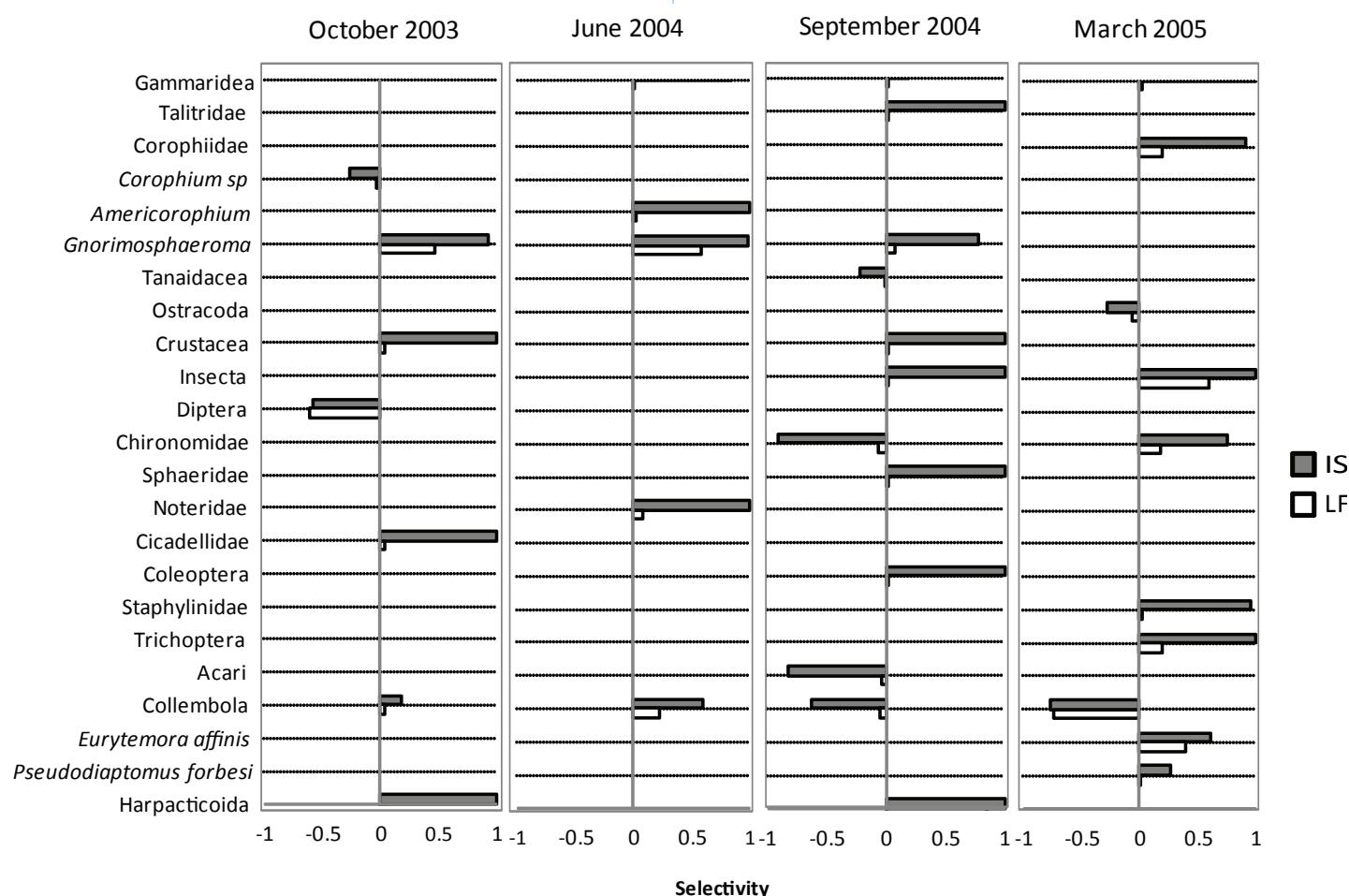


Figure 10 Selectivity indices (IS = Ivlev Selectivity Index, LFS = Linear Food Selectivity Index) for prey items identified in *Gambusia affinis* diets across dates at Browns Island

within 6 to 15 years (Levin and Talley 2000). For fish diets within marsh channels, epibenthic and benthic macroinvertebrates comprised the majority of diet components, followed by insects and zooplankton. Diet composition varied among fish species but, surprisingly, none of the fish we examined depended on zooplankton during any portion of the year. Instead, fish diets were composed predominantly of epibenthic crustaceans—amphipods, cumaceans, tanaids, and isopods—benthic polychaete worms, and aquatic insects, with just a few occurrences of planktonic copepods and cladocerans.

Neuston Community Response

We observed strong seasonal fluctuations in the community structure and abundance of the northern estuary neuston communities, a pattern also seen in estuarine-dependent fishes and zooplankton (Gewant and Bollens 2005, 2011), as well as in salt-marsh invertebrates (Balling and Resh 1991). With the exception of Collembolans, we observed that neustonic insect densities decreased dramatically in winter, and rebounded in spring through early fall. This pattern follows seasonal cycles of vascular marsh plant production, and aligns with previous findings from Petaluma Marsh, just upstream from Carl's Marsh, where peak biomass, abundance and matu-

ration of tidal marsh insect herbivores were found to occur in late spring and early summer, and were thought to be related to seasonal air temperature and the rapid rise in succulent plant biomass (*Sarcocornia virginica*) (Balling and Resh 1991). This is not surprising given that many of the most abundant members of the neuston community are herbivores, including sap feeders (Delphacidae, Cicadellidae, Aphididae, Chironomidae, and Ephydriidae) and leaf- and stem-miners (some Ephydriidae and Chironomidae larvae) (Kubátová–Hiršová 2005).

As with our data, tidal marsh herbivore communities often exhibit a sudden decline in late summer, a pattern previously noted to coincide with peak tidal inundation and salinity, both of which increase porewater salinity in marsh sediments (Balling and Resh 1991). Increasing salinity negatively affects sap-feeders, such as leaf hoppers and aphids, by increasing sap salinity in marsh succulents, thereby reducing food quality (Balling and Resh 1991). The observation that salt marsh aphids seek lower salinity plants (Regge 1973) provides insight into the temporal and spatial variability we observed in herbivorous neuston abundance in the northern estuary marshes. Pearson correlations with MDS ordination revealed that aphids and cicadellids were more strongly associated with Browns Island, Sherman Lake, and Bull Island, the three sites with the lowest salinities. Spiders (Araneae) and psocid detritivores, on the other hand, were more strongly associated with higher salinity conditions, and were prevalent at Coon Island, Pond 2A, and Carl's Marsh. Spiders have been found to be salt-tolerant in other locations, perhaps because their prey regulate the salinity of their hemolymph (Balling and Resh 1991). Psocids have been observed to increase in abundance during periods of higher salinity, suggesting that these organisms are more salt-tolerant than most detritivores which reach peak abundance during the winter or early spring (Balling and Resh 1991).

Our distance-based redundancy analysis suggests neuston communities respond strongly to temperature, salinity, season, and Delta outflow—four related

environmental variables known to affect porewater salinity, and therefore food quality for herbivorous marsh invertebrates (Balling and Resh 1991). In turn, these variables influenced the degree of community similarity among marshes across the estuarine landscape of northern estuary. During the winter and early spring, when freshwater influence is high, the neuston community at Browns Island and Sherman Lake (0.1 to 0.7 psu) strongly differed from the typically more saline communities, such as Carl's Marsh and Pond 2A (2.9 to 10 psu). In the Napa River estuary, neuston communities converged with one another during the winter high flow period (avg. similarity: $61.6 \pm 3.8\%$, 0.2 to 7.6 psu salinity range), but became more different (avg. similarity: $49.5 \pm 5.0\%$) during the summer when salinities ranged between 18 to 22 psu along the Napa salinity gradient. Our data from June sampling in 2004 and 2005 further suggest salinity, and not season alone, strongly influences neuston communities. In June 2005, an unseasonably late freshet dropped salinities to near-winter levels in the Napa River estuary (6.6 to 7.4 psu), while salinities the previous year fell between 16.63 to 18.36 psu. During the freshet, neuston communities increased in similarity to one another, coinciding with an increase in native fish species using Napa marsh channels (Gewant and Bollens 2011); both the neuston and fish communities reflected communities observed during early spring months when the estuary is characterized by low temperatures and salinity. These observations suggest that salinity plays a strong role in structuring temporal and spatial neuston community dynamics in the northern estuary.

In contrast with marsh herbivores, Collembolan abundance peaked during the winter, when it was often 8 to 100 times more numerically abundant than other taxa, a pattern also observed in North Sea salt marsh communities (Sterzynska and Ehrnsberger 2000). Because Collembola consume detritus (Hagvar 1983), principal ecological factors that govern their distribution in marsh ecosystems include soil organic matter content, litter availability (Sterzynska and Ehrnsberger 2000), and salinity, all of which affect food availability for detritivores. Seasonal fluctua-

tions in food abundance are thought to be related to plant senescence and the flushing of marsh surfaces by lower-salinity tides and rainfall which reduce the salinity content of detritus, rendering it more palatable to detritivores (Foster and Treherne 1976). While we did not measure these factors in this study, we observed that Collembola were most abundant in the west Delta and Bull Island, the three least-saline sites. Tidal freshwater and brackish marshes also tend to have higher organic carbon content, and hence, detrital abundance, compared with salt marshes (Odum 1988). Thus, in addition to lower salinities, more available detritus may further explain higher observed Collembolan abundance in the west Delta and Bull Island.

Our second overarching observation about neuston is that community assemblage appears to respond to changes in vegetation community assemblages. Specifically, one-third (7%) of total explained variation in neuston assemblage structure was related to the presence of cattail wetlands (*Typha* spp.), Pacific cordgrass (*Spartina foliosa*), and alkali bulrush (*Bulboschoenus maritimus*) within 2 m of marsh channels. We observed *Typha* spp. communities to be most strongly associated with Hymenopterans, cicadellids, corixids, chironomids, and Collembolans. These insects, as well as *Typha* spp., are most prevalent in less saline conditions. On the other extreme, saline cordgrass (*Spartina foliosa*) was most associated with spiders (Araneae), Psocoptera, and Psychodidae. As mentioned earlier, spiders and psocopterans tolerate saline conditions, which may explain their elevated abundance in sites with *S. foliosa*, a salt-tolerant plant. Although DISTLM results indicate that *Bulboschoenus maritimus* explains some of the variation in neuston assemblage structure in our study, no clear association between this plant and the neuston community was readily observable. Because *B. maritimus* is found across the salinity gradient of our marshes, while the other two vegetation types are not, the lack of strong community linkages between this plant and any particular member of the neuston supports our contention that salinity plays a stronger role in dictating neuston

community assemblage structure than does vegetation community alone. However, Levin and Talley (2000) point out that most environmental parameters do not function independently of one another; salinity gradients produce strong zonation patterns in vegetation type.

Benthic and Epibenthic Community Response

In contrast to the neuston community, the benthic/epibenthic community responded very little to seasonal shifts in temperature, salinity, and Delta outflow. Long-term salinity gradients at the estuary scale appear to be a stronger driver of benthic community dynamics, despite the large seasonal salinity fluctuations measured at the lower estuarine sites such as Pond 2A and Carl's Marsh (2.0 to 22.0 psu). Minimal seasonal shifts in benthic/epibenthic macroinvertebrate communities have previously been observed in San Francisco Bay (Nichols and Thompson 1985), as well as in the Tijuana Estuary, Sweetwater Marsh, and Los Peñasquitos Lagoon in southern California (Desmond et al. 2002), where the lack of seasonal influence on the benthic/epibenthic invertebrate community was attributed to the opportunistic nature of the invertebrate assemblage, which included spionid and capitellid worms, as well as amphipods such as *G. japonica* and Corophiidae. These organisms, which were common in our samples, mature rapidly and can reproduce many times per year. As a result, they do not track seasonal patterns (Desmond et al. 2002). However, benthic/epibenthic community structure exhibits strong seasonal trends in other systems, perhaps because more northerly estuaries experience stronger temporal differences in abiotic environmental conditions that prevent multiple reproductive events throughout the year (Johnson et al. 2007).

We observed lower abundance and diversity in benthic/epibenthic macroinvertebrates for community shifts along the salinity gradient in the west Delta, where salinities remain low throughout the year. Deep-water benthic communities in the northern estuary showed a similar pattern, with low species richness in the 5- to 8-psu salinity zone (Peterson

and Vayssières 2010). The deep-water communities also tracked Delta outflow through wet and dry years regardless of site-specific physical habitat conditions (Peterson and Vayssières 2010). This pattern is in keeping with other systems outside of San Francisco Bay, in which benthic macroinvertebrate diversity and abundance increases with increasing salinity (Odum 1988), likely because neither marine nor freshwater species are well adapted to the mesohaline salinity range (Remane and Schlieper 1971). The low-salinity benthic/epibenthic community was characterized by oligochaetes, nematodes, ostracods, the freshwater clam *Corbicula fluminea*, the isopod *G. insulare*, the polychaete worms *Fabricia* sp. and Capitellidae, and chironomid larvae. This community assemblage is characteristic of tidal freshwater marshes throughout North America, and Odum (1988) described the same suite of organisms on the eastern coast of the United States.

Sherman Lake, a restoring site in the west Delta marsh complex, exhibited the lowest benthic/epibenthic taxonomic richness and abundance of any of the six sites, including Browns Island which exhibits very similar salinities. Lower benthic/epibenthic taxonomic richness and abundance at Sherman Lake may be related to vegetation assemblage structure, which is strikingly different within channels compared to Browns Island. Channels at Sherman Lake are filled with submerged aquatic vegetation (SAV), including Brazilian waterweed (*Egeria densa*) and coon tail (*Ceratophyllum demersum*), as well as water-primrose (*Ludwigia* sp.), and water hyacinth (*Eichhornia crassipes*). As a result, channel bottoms are characterized by a dense mat of roots rather than open mud, a characteristic previously observed to affect species abundance and richness in the Delta (Toft et al. 2003). Unlike seagrass communities where rooted vascular plants lead to higher infaunal abundance and diversity (Heck 1995; Webster et al. 1998; Bostrom and Mattila 1999), increased shoot density or root structure associated with submerged aquatic macrophytes often reduces benthic invertebrate abundance in the substrate (Arocena 2007) by producing heavy detritus loads that, upon decomposition, reduce

dissolved oxygen concentrations at the sediment surface (Gordon 1998; Norkko and Bonsdorff 1996). We should note, however, that our sampling methods did not evaluate the epibenthic/epiphytic invertebrate community within SAV shoots and leaves, only sampling the sediment substrate. Given that SAV beds within the Delta have been previously observed to hold more invertebrates than open water areas, Sherman Lake likely contains a higher abundance and diversity of benthic/epibenthic invertebrates than our data suggest.

Just as the benthic/epibenthic community structure at our tidal brackish and freshwater sites aligned with patterns observed in other systems, the benthic/epibenthic community assemblages in the more saline sites mirrored observations from channel habitats in other California salt marshes (Desmond et al. 2002; Robinson et al. 2011). The more saline-tolerant community was characterized by the amphipods *G. japonica*, *S. alienense*, the cumacean *N. hinumensis*, the clam *Macoma* sp., and the polychaete worms *Eteone* sp., *Streblospio benedicti*, and Capitellidae. *S. alienense* were most abundant at Carl's Marsh, the most saline site investigated. Other studies show that this non-indigenous amphipod thrives in muddy-bottomed marsh ecosystems, and is found in particularly high abundances in China Camp marsh, located near Carl's Marsh, as well as at the estuarine turbidity zone between Suisun and San Pablo bays (Lee et al. 2003). *S. alienense*, as well as *S. benedicti* and capitellid polychaetes, respond well to stochastic disturbance and environmental stress (Thistle 1981; Levin 1984), which may explain their abundance in key salinity transition points, at young restoration sites, and in pollution-tolerant communities in southern California bays (Ranasinghe et al. 2004). Also, many of the more saline-associated organisms, including *S. alienense* and *N. hinumensis*, are thought to prefer cooler temperatures (Akiyama and Yamamoto 2004; Floerke and Templin 2011), which may partially explain their increasing abundance with distance from the Delta (Thompson et al. 2007). Finally, the Asian cumacean, *N. hinumensis*, has been previously identified as the most abundant crustacean in chan-

nel edge and slough communities of Suisun, San Pablo, and South San Francisco bays (Thompson et al. 2007). We observed this pattern during the summer in the Napa River estuary sites.

Fish Diet Response

Despite categorization of the three most prominent marsh channel fish species as pelagic transient (inland silverside), surface-feeding shallow-water resident (western mosquitofish), and demersal resident (yellowfin goby) (Gewant and Bollens 2011), benthic/epibenthic crustaceans and neustonic insects dominated their diet compositions, and were strongly selected from the available prey field, compared to zooplankton. Despite the prevalence and often high densities of calanoid copepods and cladocerans in the prey field (S.M. Bollens, WSU, unpublished data, 2013) presumably coincident with the fish occupying the marsh channels, they were consumed only rarely by most of the fish. Even the smaller size classes (<30 mm) of inland silversides indicated minimal consumption of cladocerans and copepods. Instead, the few zooplankton consumed were distributed evenly among individuals that ranged from 25 to 73 mm in length, indicating that zooplankton are not a predominant food source of silversides during the life stages which we captured. *Eurytemora affinis* appeared relatively infrequently in the diets of inland silversides (Coon Island 1/05; Pond 2A 1/05, 3/05, 6/05) and western mosquitofish (Browns Island 3/05). *Pseudodiaptomus forbesi* appeared occasionally, in inland silverside and western mosquitofish. Cyclopoids were exceedingly rare in any of the fish diets. Further, three of the most ubiquitous zooplankton species in the marsh channels—*Oithona davisae* (one of the earliest non-indigenous zooplankters to occur in San Francisco Bay), *Limnoithona tetraspina*, and *Acartia californiensis* (S.M. Bollens, WSU, unpublished data, 2013)—did not appear in the diet composition of any of the fish examined.

As habitat generalists, we expected that the three non-indigenous fishes would opportunistically exploit the broader availability of macroinvertebrates and

fish in the available prey field, thereby providing an indication of functional food web relationships between estuarine marshes and fish communities. Inland silversides that occupy estuarine marshes are documented to be eclectic feeders, with broad ontogenetic variation (Cadigan and Fell 1985), but Visintainer et al. (2006) described the diet composition of inland silversides in the marsh channels of China Camp to comprise 99% amphipod parts, *S. alienense*, *N. hinumensis*, and delphacid homopterans—comparable to what we found. The cosmopolitan yellowfin goby, which now occupies almost all tidal environments of the Bay-Delta is considered to be an ambush or search feeder (Kikuchi and Yamashita 1992; Workman and Merz 2007) that feeds opportunistically on mysids and amphipods (Feyrer et al. 2003). Cohen and Bollens (2008) reported results from our three Napa River sites (Coon Island, Bull Island, and Pond 2A) and found the diet of silversides was primarily composed of copepods, cumaceans, and flying insects, while yellowfin goby diets were composed of annelids, cumaceans, and amphipods; very similar to what we found. In contrast to our results, Cohen and Bollens (2008) reported few to no corophiids in the diets of these fishes. At a central Delta site (Liberty Island) upstream of our sampling sites, Whitley and Bollens (2013) found inland silversides consumed amphipods (*Corophium* sp.) and insects (chironomid larvae) in spring, primarily insects (*Corixidae* nymphs and juveniles) in summer, and zooplankton (*Daphnia* sp. and *Pseudodiaptomus forbesi*) and amphipods (*Corophium* sp.) in winter; yellowfin goby consumed insects (chironomid larvae), plant detritus and sediment in summer. *Gambusia* spp. are described as typically feeding at the water surface, perhaps reflecting their dorsally-oriented mouth and dorso-ventrally flattened head (Lewis 1970; Pyke 2005). This contrasts with our diet results, which indicate that *G. affinis* fed largely upon benthic/epibenthic prey, except during periods of high freshwater flow when they strongly selected for copepods in the water column (*E. affinis*).

Compared to the diverse and often dense zooplankton and neustonic insects found in the marsh channels,

fish predation concentrated extensively on benthic/epibenthic crustaceans suggests that either the rarer, more selected benthic/epibenthic prey were not representatively sampled with our sampling techniques, or that the relatively high water turbidity in the channels inhibited visual foraging on copepods and surface drift insects, but was less inhibitory for predation on the benthic/epibenthic crustaceans. In addition to general reference to turbidity inhibiting predation on estuarine copepods (Benfield 2012), there is strong evidence that visual feeders shift their feeding from surface drift invertebrates to benthic prey under turbid conditions (Harvey and White 2008), despite evidence that semi-aquatic dipteran larvae and other marsh insects are almost twice as energy rich as crustacean prey (Gray 2005). In line with previous research showing an ecologically meaningful distinction between 2-D and 3-D consumers (Pawar et al. 2012), strong selection by estuarine fishes for benthic/epibenthic prey may thus indicate that the arguably simplified habitat structure in which benthic/epibenthic prey live (2-D feeding plane along marsh channel bottoms versus 3-D feeding plane in the water column) may be a particularly important determinant of fish feeding selectivity in the turbid northern estuary tidal marsh ecosystems. Additional factors that may also influence prey selection include prey body size, mobility, density, distribution, and quality (i.e., energy content) (Gray 2005; Zhao et al. 2006). However, when estuarine fishes have turbidity-caused visual impairment may reduce the influence of these factors may influence prey selectivity less (Koski et al. 2003; Carter et al. 2010).

CONCLUSIONS

In comparison with other studies, the suite of environmental variables examined in this study explains relatively little of the variation associated with neuston and benthic macroinvertebrate community structure. We were able to account for 21.9% of the variation in neuston community structure and 35.4% of benthic macroinvertebrate community structure. While few prior studies have related environmental

variables with tidal marsh invertebrate communities, those examining benthic macroinvertebrates generally explain 70% to 80% of observed variation (Desmond et al. 2002; Nanami et al. 2005; Degraer et al. 2008; Kanaya and Kikuchi 2008; Tomiyama et al. 2008). In addition to salinity, some of the key factors driving benthic macroinvertebrate distributions in other estuarine systems include sediment grain size, oxidation-reduction potential, and silt-clay content (Desmond et al. 2002; Nanami et al. 2005; Degraer et al. 2008; Kanaya and Kikuchi 2008). Oxygen concentration, belowground biomass or root density, elevation of habitat, and sediment organic content also influence benthic/epibenthic macroinvertebrate community structure, but to a lesser extent (Talley and Levin 1999; Tomiyama et al. 2008). In contrasting our data with other work, we conclude that benthic/epibenthic macroinvertebrates and neustonic insects respond primarily to their environment at small (<10 m), site specific scales, because the landscape-scale environmental drivers examined in this study explain much less variation in invertebrate community structure than site-specific variables examined in other studies.

In addition to these site-specific environmental characteristics, our results show that estuarine benthic/epibenthic and neustonic macroinvertebrate communities respond secondarily to landscape-scale environmental drivers. Enduring site variables—such as channel sinuosity, site area, channel edge, or channel density—explained little to none of the variation observed in marsh macroinvertebrate communities. In contrast, position along the estuarine salinity gradient, which influences primary producer communities, combines with temporal variation in primary production, freshwater flow, and temperature to create a suite of environmental conditions that control the community structure of estuarine neuston and benthic/epibenthic macroinvertebrates. It thus appears that meso-scale characteristics may influence the structure of marsh invertebrate communities less than variability in micro-scale characteristics, such as sediment grain size, or macro-scale characteristics, such

as drought versus flood years for the Sacramento and San Joaquin rivers.

Our analysis of diet composition and selectivity for inland silversides (*M. beryllina*), yellowfin goby (*A. flavimanus*), and western mosquitofish (*G. affinis*) collected from interior marsh channels suggests that benthic/epibenthic prey comprise an important and temporally stable prey base for estuarine fishes in these habitats, with supplementation from neustonic invertebrates in the spring and summer. These findings generally support other documentation of fish foraging in estuary marshes, especially the focus on epibenthic/benthic crustaceans—amphipods, cumaceans and mysids—and the general scarcity of pelagic zooplankton (Visintainer et al. 2006). Therefore, we suggest that restoration planners should consider tidal channels and mudflats as important habitat features that bolster food web support and promote them in restoring marshes because of their importance as sources of benthic/epibenthic production. Although we could not attribute much variation in the predominant epibenthic/benthic fish prey to the various aspects of tidal channel geomorphology, Barry et al. (1996) and Visintainer et al. (2006) reported that marsh fishes fed upon some of these taxa (e.g., cumaceans) in higher-order channel systems. Furthermore, channels with bordering vegetation promote input of neustonic insects that are also important, energetically-rich sources of prey, especially for fish species of concern. For example, juvenile Chinook salmon, *Oncorhynchus tshawytscha*, are widely known to feed extensively on aquatic insects throughout their estuarine residency and outmigration (Simenstad et al. 1982; Schreffler et al. 1992; Gray et al. 2002), which occurs between February and April in the estuary (McFarlane and Norton 2001). During this time, we observed increasing densities of chironomid larvae in interior marsh channels, the emergent or adults of which dominated the neuston assemblage in March. While Chinook do not remain insect feeders throughout their early, coastal life cycle, their reliance on food resources generated in vegetated tidal marsh ecosystems highlights the importance of these areas to estua-

rine dependent fishes, many of which utilize marsh ecosystems at critical points in their life histories (Nobriga et al. 2005).

Zooplankton, by contrast, were less consistently fed upon by the three species of fish considered in this study, regardless of their feeding mode, suggesting that zooplankton availability may be more variable in space and time within marsh ecosystems, or that conditions within marsh channels (i.e., turbidity) make it difficult for fish to prey on these food sources. Calanoid copepods (i.e., *Eurytemora affinis*) were most frequently consumed under low salinity conditions, which indicates that zooplankton may be more available to fish under low temperature, high-freshwater flow conditions—the same conditions a complementary study by Gewant and Bollens (2011) observed to coincide with higher native fish abundance in interior marsh channels. Though our use of non-native fishes to examine the functional role of tidal marsh ecosystems in supporting estuarine food webs may have limited applicability to native fishes, emerging evidence from native tule perch (*Hysterocarpus traski*) indicate that benthic/epibenthic crustaceans can comprise the majority of native fish diets in interior marsh channels as well (Appendix D).

Our results not only establish that channelized, vegetated, shallow-water ecosystems within the northern estuary support estuarine food webs through both epibenthic/benthic and neustonic invertebrate production, they also indicate that restoring tidal marsh ecosystems such as Pond 2A and Bull Island on the Napa River, and Carl's Marsh on the Petaluma River, appear to function similarly to reference sites throughout the northern estuary. These marshes vary in age (10 to 50 years since restoration), elevation, and vegetation species diversity (Williams and Orr 2002; Tuxen et al. 2011), yet in terms of invertebrate assemblages and fish diets, appear to provide similar prey resources to marsh channel fish species that represent of pelagic transient, shallow-water surface feeding resident, and demersal-resident life histories. These results corroborate other breached-levee res-

toration studies in which prey availability and fish growth were comparable in all sites regardless of restoration status (Nemerson and Able 2005; Able et al. 2008; Cohen and Bollens 2008).

Within the estuary, tidal marsh ecosystems are well recognized for their significance as fish and wildlife habitat (Skinner 1962; Warnock and Takekawa 1995; Meng and Matern 2001; Matern et al. 2002; Brew and Williams 2010; Demers et al. 2010; Gewant and Bollens 2011; Athearn et al. 2012; Thorne et al. 2012), but much less consideration has been directed toward the potential for these ecosystems to serve as a pillar of food web support for the greater estuary (Sobczak et al. 2005; Stepanauskas et al. 2005; Howe and Simenstad 2007; Cohen and Bollens 2008; Grimaldo et al. 2009; Howe and Simenstad 2011). Food limitation has been suggested as a contributing driver of the POD, but conceptual models focus on food web linkages among fish, zooplankton and phytoplankton, rather than the trophic role of detritus-based food webs associated with emergent tidal marsh wetlands (Sommer et al. 2007). Many POD species, however, rear and spawn in tidal marsh wetlands, including striped bass (*Morone saxatilis*), which our data show rely heavily on benthic/epibenthic macroinvertebrates associated with shallow-water, vegetated ecosystems (Appendix D). Given that phytoplankton production is limited in the San Francisco Estuary compared to other estuaries (Kimmerer and Orsi 1996; Jassby et al. 2002), our data suggest that energy translated from interior marsh ecosystems may potentially provide a supplemental source of food web support for a stressed estuarine food web.

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