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Fish assemblages across a vegetation gradient in a restoring tidal freshwater wetland: diets and potential for resource competition

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Abstract Marsh habitats have been the focus of recent worldwide restoration efforts due to their degradation and destruction as a result of human development. We assessed fish resource use at a naturally restoring marsh (Liberty Island, California, USA) by comparing diet composition, stomach fullness, normalized stomach weight, and diet overlap across a vegetation gradient. Fish were collected using gill nets and fyke nets at six sites during spring 2010, summer 2011 and winter 2012. We analyzed 392 stomachs from the eleven most abundant species collected. Prey composition and biomass varied seasonally for all fish species, but there were no notable differences across sites or seasons for stomach fullness or normalized stomach weight for most fish species. Results from non-metric multidimensional scaling (NMDS) and two-way analysis of similarities (ANOSIM) indicated minimal diet overlap between species (R=0.633, p=0.001) and seasons (R=0.413, p=0.001). Seasonal habitat and resource use across the vegetation gradient was species-specific. Small but significant spatial diet differences were detected for inland silverside, striped bass and bigscale logperch. Delta smelt exhibited seasonal diet differences by shifting from chironomids and zooplankton during spring, to amphipods and zooplankton during winter. More generally, fish maintained stomach fullness across all sites and seasons while maintaining minimal dietary overlap. Our study emphasizes the importance of tidal marshes as feeding habitat for several fish species, including the endangered delta smelt.

Keywords Wetland restoration · Tidal marsh · Fish ecology · Diet · Competition · Resource partitioning

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Introduction

Habitat type and complexity (e.g., tidal channels and vegetated patches) influence resource use by many fish species (Minello et al. 1994; Peterson and Turner 1994; Kneib 1997; Okun and Mehner 2005; Visintainer et al. 2006). For instance, Humphries and Potter (1993) found that the elongated hardyhead (Atherinidae) and the long-headed goby (Gobiidae) both primarily consumed grass shrimp in submerged aquatic vegetation, while in bare sand they consumed amphipods and nereid polychaetes. More broadly, habitat heterogeneity may modify the outcome of biological interactions such as competition and predation (Coen et al. 1981; Danielson 1991). Many fish species utilize tidal wetlands and marsh habitat extensively, benefiting from high resource availability and reduced predation pressure, resulting in increased growth rates (Weinstein and Walters 1981; Boesch and Turner 1984; Minello 1993; Kneib 1997; Simenstad et al. 2000; Ribeiro et al. 2004; Cohen and Bollens 2008).

The San Francisco Estuary (SFE; defined here as the San Francisco Bay and the tidally influenced portions of the Sacramento and San Joaquin Rivers) is one of

the most highly altered and species-invaded estuaries in the world (Nichols et al. 1986; Cohen and Carlton 1998; Lotze et al. 2006; Dallas and Barnard 2009; Bollens et al. 2011). Levees have been constructed within the Sacramento-San Joaquin Delta (hereafter "Delta"; the freshwater portion of the SFE, part of which is tidally influenced) to divert freshwater flow for agricultural, municipal, and industrial purposes (Pimentel et al. 1997; Mount and Twiss 2005; Lund et al. 2007). As a result, over 90 % of wetlands within the SFE have been removed from tidal inundation, resulting in extreme modifications in water quality and habitat structure (Kimmerer 2002; Matern et al. 2002; Hammersmark et al. 2005). At the same time, native fish species have experienced larger declines than non-native species (Matern et al. 2002; Brown and Michniuk 2007), causing concern among fisheries agencies and prompting large-scale restoration programs within the SFE (Nobriga et al. 2005; Moyle 2008).

In an effort to improve ecosystem health in the SFE, restoration of tidal freshwater marsh ecosystems by reconnecting regions currently managed for agricultural purposes to their adjacent rivers and sloughs has been proposed (CALFED 2000). One restoration method currently employed is the breaching of levees in the Delta (Simenstad et al. 2000; Florsheim and Mount 2002). Breaching levees creates natural floodplains and reintroduces tidal inundation, favoring some fish species. For instance, Lindberg and Marzuola (1993) documented the presence of spawning delta smelt (a federally listed species) near levee breaches in a flooded island restoration project in the northwestern Delta, and Whitley and Bollens (in review) reported on the fish assemblage along a vegetation gradient in a restoring freshwater tidal wetland in the Delta. However, little is known about fish resource use (including prey resources) in these tidal wetlands after breaching has occurred.

Here we examine the diet of several fish species across a vegetation gradient in a restoring tidal wetland in the Delta. Our overall objective was to compare the diets of several fish species across a vegetation gradient during several seasons to determine what type of food resources fish consumed in these previously understudied shallow freshwater habitats. Such information is needed to evaluate tidal wetland habitat restoration effectiveness, which in turn will allow managers to formulate conservation strategies for species of special concern, such as delta smelt.

Materials and methods

Study site

The Delta experiences a Mediterranean climate with a dry, warm period from May through October and a cool, wet period from November through April. Liberty Island, once used for agriculture, is now an inundated island approximately 21 km^2, located in the southern portion of the Yolo Bypass, California (38.1749 N, -121.4043 W) (Fig. 1). The Island is positioned at the confluence of many sloughs (commonly referred to as the Cache Slough Complex) where it is inundated by nutrient rich water (Lehman et al. 2010) and encounters massive seasonal freshwater flows from the Yolo Bypass (Marchetti and Moyle 2001; Sommer et al. 2001a, b). Liberty Island is one of the few perennially flooded, naturally restoring islands in the Delta, with a broad gradient in tidal elevation, stream flow exposure and structural heterogeneity. Water depth in the northern portion of the island is approximately 1 m during mean high water tide. During low tide, the northwestern portion of the island consists of exposed tule marsh and large mudflats, while the southern and eastern portions remain continuously submerged. Numerical hydrodynamic modeling of Liberty Island indicates that the eastern side receives considerably greater stream flow exposure and wave energy than does the western side, with a specific gradient represented by our three sampling zones (described further below) (Matt Brennan, Environmental Science Associates – Philip Williams & Associates, unpubl. data).

Levees were breached on the south end of Liberty Island due to river flooding following a heavy rain event in early 1998 (Lehman et al. 2010). Historic hydrological cycles were re-established, allowing natural flood pulses through the wetland and increased disturbance of the site. Stream flow, tidal exposure, and elevation have allowed emergent vegetation to recolonize more rapidly in the western and northern portions of the island and more slowly in the eastern portion of the island, thus creating a west (high) to east (low) emergent vegetation gradient (Fig. 1). Tule (*Schoenoplectus acutus* and *S. californicus*) and cattail (*Typha latifolia*) structure the majority of the marsh habitat (Mark Hester, University of Louisiana at Lafayette, pers. comm.). The west side of the Island is exposed during low tide and contains dense mud and

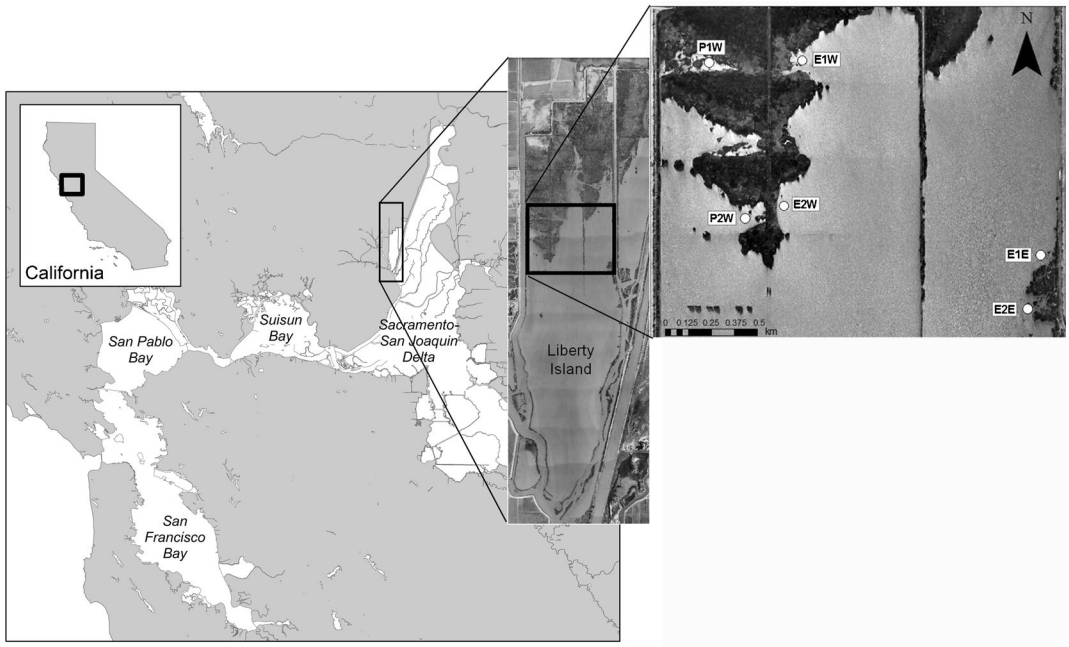

Fig. 1 Liberty Island, California, is located in the upper Sacramento-San Joaquin Delta at the south end of Yolo Bypass, adjacent to Prospect Island and Little Holland Tract. *Circles* represent each site, *PW* protected west, *EW* exposed west, *EE* exposed east

agricultural clay, while the east side is continuously submerged and contains soft mud (US Fish and Wildlife Service, unpubl. data). The island currently supports wildlife such as beavers (*Castor canadensis*), waterfowl and other birds (e.g., sandhill cranes, *Grus canadensis*) migrating along the Pacific Flyway, and has outstanding potential for restoration, floodplain management and endangered species recovery (Lund et al. 2007).

Fish sampling

Fish were collected across three sampling zones based on a gradient of high to low emergent vegetation density (and conversely, low to high stream flow exposure): (1) protected west (PW) > (2) exposed west (EW) > (3) exposed east (EE) (Fig. 1). Zone PW was densely vegetated and contained low stream flow exposure due to the adjacent intact levee on the west side of the island. Zone EW was moderately vegetated and contained moderate stream flow exposure. Zone EE was mostly open water with smaller patches of vegetation and contained high stream flow exposure due to the close proximity of a major levee break on the east side of the island. Each zone contained two sampling sites, one in the north end of the zone and one in the south end, providing six sampling sites total (Fig. 1).

During each of three seasonal samplings — spring (March 28–April 2, 2010), summer (August 14–19, 2011) and winter (February 7–12, 2012) — fish collection occurred over six consecutive days, with one site sampled per day. We deployed three experimental gill nets (seven panels with mesh sizes ranging between 12.7 and 101.6 mm, knot to knot) and one or two fyke nets (3.1 mm mesh), depending on emergent vegetation structure and presence of channels at each site. All nets were set in early morning at high tide and fished through the ebbing tide with an average of 5.5 h of soak time for each net set. The sites on the west side of the island were exposed during low tide, while the sites on the east side of the island were submerged approximately 0.5–1 m at low tide. Following low tide, fish were removed from the nets, identified to species, enumerated, anesthetized with MS-222 (tricaine methanesulfonate, Sigma), preserved in 10 % formalin and brought back to the laboratory for later analyses. Fish with fork length (FL) measuring >160 mm were measured live in the field, while fish with FL <160 mm were measured in the lab after preservation.

Fish stomach processing

We examined 392 fish stomachs from the eleven most abundant species collected at Liberty Island using

gravimetric methods as described by Hyslop (1980). The FL and body weight of each fish was measured to the nearest mm and 0.1 mg, respectively. The stomach of each fish was removed, rinsed with deionized water, blotted dry and weighed (wet) to the nearest 0.1 mg. Percent stomach fullness was assessed and assigned a relative index of fullness (1= empty, 2= < 25 % full, 3= 25 % full, 4= 50 % full, 5= 75 % full, 6= 100 % full). In addition, the extent of digestion of stomach contents was assessed and assigned a relative index (1= nothing identifiable, 2= < 25 % identifiable, 3= 25–50 % identifiable, 4= 50–75 % identifiable, 5= 75–100 % identifiable, 6= 100 % identifiable). Prey items were sorted, enumerated, and identified to the lowest feasible taxonomic category (Table 1). Benthic and planktonic crustaceans were identified to genus or species while other major prey items, such as insects, were identified to order or family (Ward and Whipple 1959; Lehmkuhl 1979). All prey items within each taxonomic group from each stomach were combined and weighed to the nearest 0.1 mg.

Stomach content weight was normalized by dividing each individual stomach weight (mg) by the individual fish weight (mg), termed the normalized stomach content weight.

Statistical analyses

All non-empty stomachs were pooled by fish species and site. We calculated the percent biomass of all prey taxa eaten by each fish species at each site by dividing the total weight of each prey taxon by the total weight of all prey taxa. Twelve categories were chosen (Table 1): amphipods, cladocerans, copepods, crustacean parts, decapod parts, detritus, fish, insects, molluscs, mysids, sediment, and other (e.g., nematodes, annelids, isopods, etc.). Stomach content data, stomach fullness, and normalized stomach content weight for the eleven most abundant species are shown in Table 2.

Stomachs from the eleven most abundant fish species collected were used for multivariate analyses. We examined fish diet overlap using non-metric multidimensional scaling (NMDS) using PRIMER for Windows statistical software (Clarke 1993). NMDS is an ordination technique that uses a Bray-Curtis matrix of ranked similarities and displays samples in low-dimensional space while retaining as nearly as possible the similarity rankings between groups. NMDS results were considered to represent a useful model if two-dimensional stress was less than 0.2 (stress varies from 0 to 1; Clarke and Warwick 2001).

We tested for differences in diet overlap using analysis of similarities (ANOSIM) using PRIMER for Windows statistical software (Clarke 1993). Gravimetric prey percentages were arcsine square-root transformed and a Bray-Curtis similarity matrix was used for multivariate analyses. A two-way ANOSIM was used to test for differences in diet among the nine most abundant species

Table 1 Names, categories and descriptions of combined prey categories used in diet analyses

Category	Description
Amphipods	All amphipods (almost exclusively *Corophium* sp.)
Cladocerans	All cladocerans, including *Bosmina longirostris, Ceriodaphnia dubia,* and *Daphnia* sp.
Copepods	All calanoid copepods, including *Eurytemora affinis,* Diaptomidae, *Osphranticum labronectum, Pseudodiaptomus forbesi* and *Sinocalanus doerri;* All cyclopoid copepods, including *Limnoithonia tetraspina;* All harpacticoid copepods, including *Mesochra* sp.; and all copepodites
Crustacean parts	All digested parts that could only be identified to the subphylum Crustacea
Decapod parts	All shrimp, including *Exopalaemon modestus, Palaemonetes* sp. and Palaemonidae; All crayfish, including the superfamily Astacoidea and *Procambarus clarkii*; and identifiable parts of shrimp and crayfish
Detritus	Algal and plant material
Fish	All fish species, including *Dorosoma petenense, Gambusia affinis, Menidia beryllina, Micropterus salmoides, Percina macrolepida,* and identifiable parts of digested fish
Insects	All larval and adult insects (almost exclusively larval chironomids and Corixidae nymphs)
Mollusca	All molluscs (almost exclusively Bivalvia)
Mysidae	All mysid shrimp (almost exclusively *Neomysis mercedis*)
Sediment	All mud and sand particles
Other	All annelids, fish and invertebrate eggs, isopods, nematodes, oligochaetes, ostracods and polychaetes

collected as well as across seasons and sites for each species individually. ANOSIM, similar to ANOVA, uses randomization techniques to determine the average of all ranked dissimilarities among and within groups (Global-R). The sample statistic, R (analogous to the *F* value in an ANOVA), is scaled between 0 and 1, with zero representing no difference among groups and values close to 1 indicating greater differences among groups (*R*=1 is the greatest dissimilarity possible). ANOSIM gives the significance level of R, similar to the ANOVA *p*-value, which is derived using random permutations of the similarity matrix and is calculated as the probability that a greater R could be achieved from random combinations of the data (Anderson 2001; Clarke and Warwick 2001). If the R statistic was significant at $p<0.05$ (i.e., the null hypothesis that no difference between groups exists is rejected), then pairwise post-hoc comparisons were computed using similarity percentages (SIMPER) to identify the prey taxa contributing to the differences in diet. The SIMPER procedure used Bonferroni corrected *p*-values to calculate the average dissimilarity between two fish species and how much each prey taxon contributed to the average dissimilarity (Clarke and Warwick 2001).

Results

Diet composition

Prey composition of the four most abundant fish species collected at Liberty Island varied seasonally (Fig. 2) and spatially (Fig. 3). Insects were generally consumed more in more densely vegetated sites, while amphipods were consumed more in less vegetated sites. Inland silversides consumed mostly amphipods (*Corophium* sp.) in spring, however they consumed more insects (primarily chironomid larvae) at site P1W. In summer, inland silversides consumed mostly insects (primarily Corixidae juveniles and nymphs) and in winter they consumed zooplankton (*Daphnia* sp. and *Pseudodiaptomus forbesi*) and amphipods (*Corophium* sp.). Carp consumed primarily molluscs in spring and summer at sites E2W, E1E, and E2E. Bigscale logperch consumed amphipods (*Corophium* sp. and *Gammarus daiberi*) in spring and summer at sites E2W, E1E, and E2E, and insects (Odonata nymphs, chironomid larvae, and Diptera larvae) and amphipods (*Corophium* sp.) in winter at site E1E. Striped bass consumed insects and mysids in spring at sites E1E and E2E. In summer, they consumed small-bodied fish (inland silversides, bigscale logperch, and juvenile largemouth bass) and decapods (crayfish and Palaemonidae shrimp) at nearly all sites, they consumed insects (chironomid larvae and Corixidae nymphs) only at site P2W, and smaller striped bass consumed copepods at site E2E. In winter, striped bass consumed mostly amphipods (*Corophium* sp.).

Prey composition of the remaining seven most collected fish species also varied (Table 2). White catfish consumed sediment, plant detritus, amphipods (*Corophium* sp.), fish (primarily threadfin shad), and crayfish. Delta smelt consumed cladocerans (*Bosmina longirostris, Ceriodaphnia dubia,* and *Daphnia* sp.), copepods (*P. forbesi, Eurytemora affinis*, and cyclopoids), insects (chironomid larvae), amphipods (*Corophium* sp.), and mysids. Tule perch consumed insects (Corixidae nymphs and Diptera larvae), amphipods (*Corophium* sp.), plant detritus, and other prey (isopods). Splittail consumed molluscs, sediment, and insects. Threadfin shad consumed copepods (harpacticoids), sediment, plant detritus, and other prey items (ostracods). Yellowfin goby consumed insects (chironomid larvae), plant detritus, and sediment. Hitch consumed insects (Corixidae nymphs).

Stomach fullness index and normalized stomach content weight

Mean fish stomach fullness ranged from a mean of 2 (< 25 % full) for threadfin shad to a mean of 4 (50 % full) for most fish species (Table 2). Mean normalized stomach content weights ranged from 0.02 for delta smelt to 0.09 for white catfish (Table 2).

Intra-specific diet overlap

Of the eleven most abundant species, only three species (inland silverside, striped bass, and bigscale logperch) had sufficient sample sizes and exhibited significant intra-specific diet differences.

Inland silverside Results from a 2-way ANOSIM (site x season) indicated significant differences in diet of inland silverside for both site ($R=0.20$, $p=0.001$) and season ($R=0.60$, $p=0.001$). SIMPER indicated significant site differences were due to larger diet contributions by insects (mostly Corixidae and chironomid larvae) at sites P1W (89 %) and P2W (100 %), and larger proportions of amphipods (mostly *Corophium* sp.) at sites E2W (45 %), E1E (49 %) and E2E (46 %).

Table 2 Fish species, mean fork length (mm) and range, mean stomach fullness, mean normalized stomach content weight, % prey biomass and % occurrence for all prey taxa

Fish species	Fork length (mm)		Mean stomach fullness	Mean norm. stomach content wt.	Amphipods		Cladocerans		Copepods		Crustacean parts		Decapod parts		Detritus
	Mean	Range			% prey biomass	% occurrence	% prey biomass	% occurrence	% prey biomass	% occurrence	% prey biomass	% occurrence	% prey biomass	% occurrence	% prey biomass
Inland silverside, *Menidia beryllina*	76	36–91	4	0.03	28.6	49.9	10.2	48.7	8.6	50.9	5.2	11.2	0.0	0.0	2.1
Common carp, *Cyprinus carpio*	559	10–770	3	0.03	1.3	40.7	0.0	0.0	0.0	0.0	0.0	3.8	0.0	0.0	28.4
Bigscale logperch, *Percina macrolepida*	75	64–93	4	0.04	60.4	87.4	0.1	8.9	2.0	48.9	2.1	5.6	1.0	2.2	19.7
Striped bass, *Morone saxatilis*	371	46–830	3	0.04	22.5	58.3	0.0	0.0	3.5	7.6	5.8	19.7	17.0	7.6	7.9
White catfish, *Ameiurus catus*	322	42–490	4	0.09	21.0	72.2	0.0	0.0	0.0	0.0	0.1	2.6	4.0	19.9	43.5
Delta smelt, *Hypomesus transpacificus**	69	62–76	3	0.02	14.7	47.4	24.8	90.6	34.9	80.8	5.5	15.0	0.0	0.0	2.1
Threadfin shad, *Dorosoma petenense*	74	34–137	2	0.05	0.8	1.8	8.0	49.1	9.1	49.6	21.2	30.3	0.0	0.0	33.9
Tule perch, *Hysterocarpus traski**	118	82–146	4	0.03	50.0	92.9	0.0	16.7	0.0	50.0	6.4	7.1	0.0	0.0	11.2
Sacramento splittail, *Pogonichthys macrolepidotus**	170	46–299	4	0.03	4.0	33.9	0.0	0.0	0.0	0.0	0.9	12.5	0.0	0.0	7.6
Hitch, *Lavinia exilicauda**	180	150–213	4	0.05	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	8.2
Yellowfin goby, *Acanthogobius flavimanus*	85	51–114	4	0.04	3.9	33.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	12.0

Fish species	Detritus	Fish		Insects		Mollusca		Mysidae		Sediment		Other	
	% occurrence	% prey biomass	% occurrence	% prey biomass	% occurrence	% prey biomass	% occurrence	% prey biomass	% occurrence	% prey biomass	% occurrence	% prey biomass	% occurrence
Inland silverside, *Menidia beryllina*	13.4	0.0	0.0	39.5	68.4	0.0	1.4	0.8	0.3	3.7	5.9	1.5	24.4
Common carp, *Cyprinus carpio*	94.4	0.0	1.9	0.4	22.2	40.8	86.8	0.0	0.0	27.6	45.5	1.5	29.6
Bigscale logperch, *Percina macrolepida*	44.2	0.0	0.0	11.0	29.6	0.0	0.0	0.0	0.0	1.6	15.9	2.0	20.7
Striped bass, *Morone saxatilis*	33.1	20.6	13.6	9.6	11.4	0.0	0.0	5.3	12.5	2.6	15.7	5.4	28.4
White catfish, *Ameiurus catus*	91.9	5.3	23.6	1.2	36.6	0.1	70.1	0.0	2.6	24.0	42.3	0.9	63.8
Delta smelt, *Hypomesus transpacificus**	3.8	0.0	0.0	15.2	50.4	0.0	0.0	2.3	5.6	0.0	0.0	0.5	17.1
Threadfin shad, *Dorosoma petenense*	36.8	3.5	1.8	4.2	19.3	0.0	0.0	0.0	0.0	13.2	18.9	6.2	36.4
Tule perch, *Hysterocarpus traski**	64.3	0.0	0.0	26.8	45.2	2.7	38.1	0.0	0.0	0.6	14.3	2.3	57.1
Sacramento splittail, *Pogonichthys macrolepidotus**	41.1	0.0	12.5	8.2	39.3	19.3	32.1	0.0	0.0	57.6	92.9	2.4	85.7
Hitch, *Lavinia exilicauda**	28.6	0.0	0.0	27.0	85.7	0.0	0.0	0.0	0.0	64.8	42.9	0.0	0.0
Yellowfin goby, *Acanthogobius flavimanus*	55.6	0.0	0.0	63.4	77.8	0.0	0.0	0.0	0.0	19.2	66.7	1.5	44.4

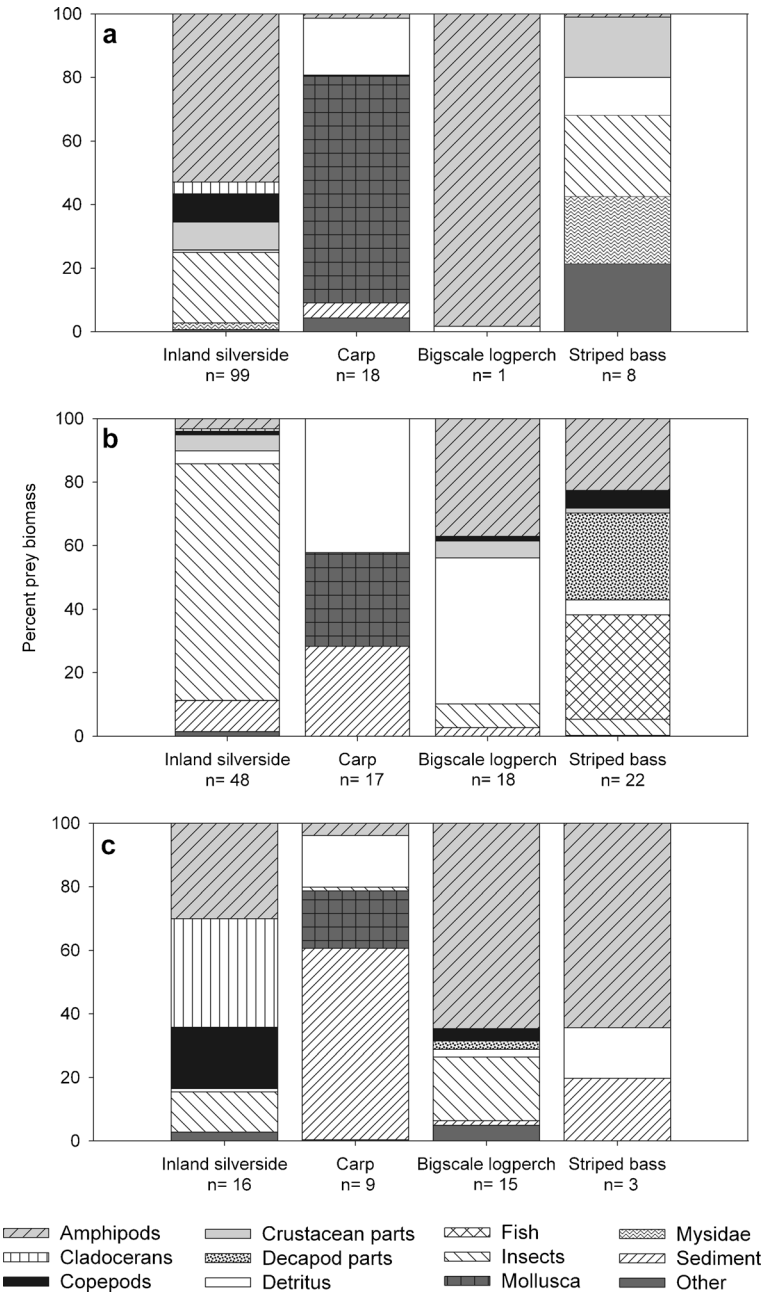

Fig. 2 Seasonal variation in stomach content composition by weight (% of total biomass) for (**a**) spring 2010, (**b**) summer 2011 and (**c**) winter 2012, pooled by fish species

Significant seasonal differences in diet were due to larger proportions of amphipods (mostly *Corophium* sp.) during spring 2010 (60 %) and winter 2012 (42 %) compared to large proportions of insects (mostly Corixidae) (96 %) during summer 2011 and a larger contribution of cladocerans (mostly *C. dubia* and *Daphnia* sp.) (31 %) and copepods (mostly copepodites) (14 %) during winter 2012.

Striped bass Results from a 2-way ANOSIM (site x season) indicated significant differences in diet of striped bass for both site (R=0.19, p=0.02) and season (R=0.25, p=0.03) with fish prey removed from analysis due to outlier indication. SIMPER indicated significant site differences were due to large diet contributions by amphipods (mostly *Corophium* sp.) at sites E1W (100 %) and E2E (60 %), and a large proportion of

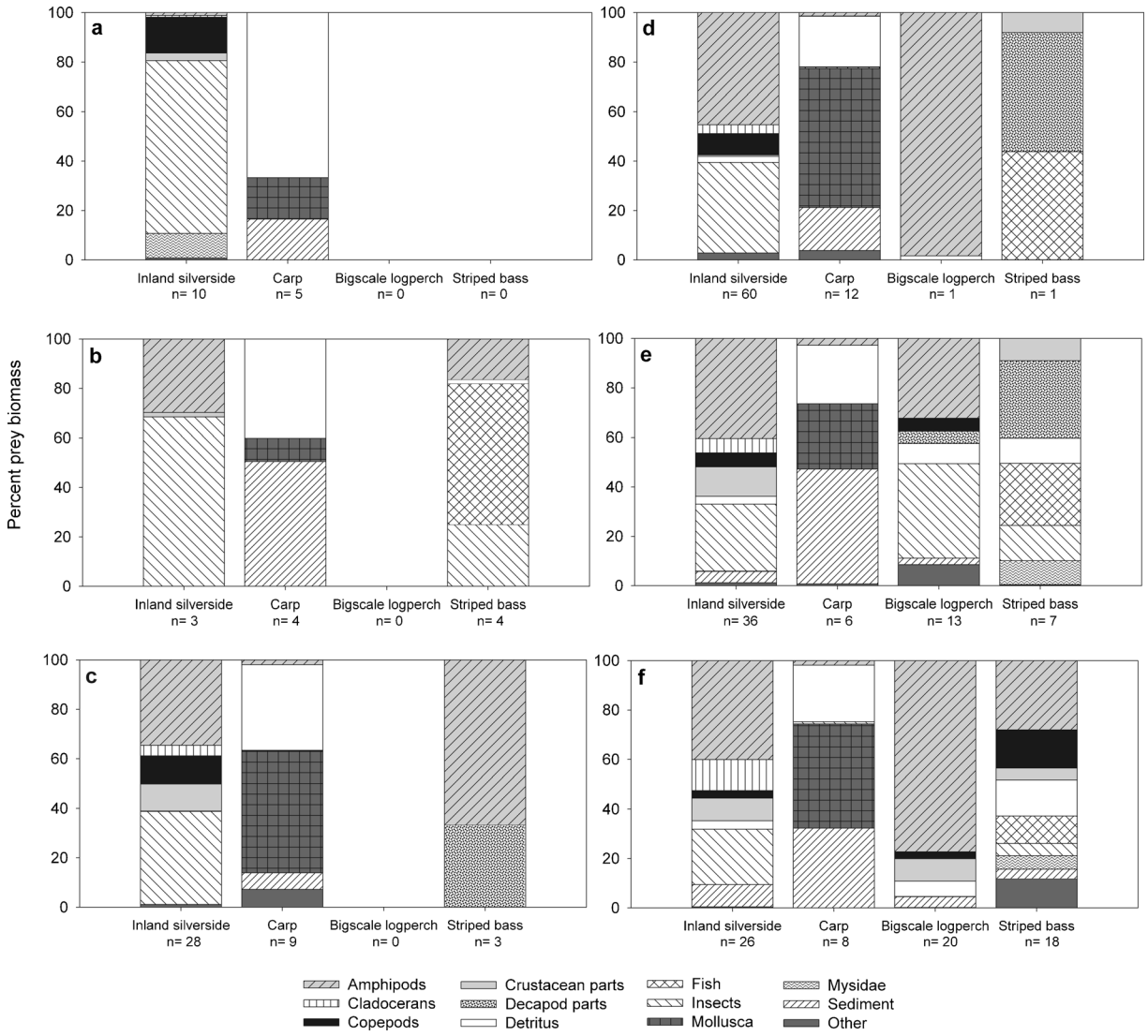

Fig. 3 Spatial variation in stomach content composition by weight (% of total biomass) for (**a**) P1W, (**b**) P2W, (**c**) E1W, (**d**) E2W, (**e**) E1E and (**f**) E2E, pooled by fish species

decapod parts (mostly Palaemonidae shrimp and Astacoidea crayfish) at site E1E (47 %). Significant seasonal differences in diet were due to larger proportions of "other" prey items (mostly nematodes) (32 %) and crustacean parts (31 %) during spring 2010 compared to large proportions of amphipods (mostly *Corophium* sp.) (36 %) during summer 2011 and winter 2012 (100 %).

Bigscale logperch Results from a 2-way ANOSIM (site x season) indicated significant differences in diet of bigscale logperch for site only (R=0.40, p=0.04). SIMPER indicated this difference was due to larger diet contributions by insects (mostly chironomid larvae) (52 %) and amphipods (mostly *Corophium* sp.) (30 %) at site E1E and larger proportions of amphipods (mostly *Corophium* sp.) (85 %) at site E2E.

Inter-specific diet overlap

Striped bass and white catfish were initially shown to be outliers on the NMDS ordination due to their piscivorous feeding behaviors, and thus were removed from subsequent multivariate analysis. Using the diets from the remaining nine most abundant fish species, NMDS analysis resulted in a useful model with a stress

of 0.16 for a two-dimensional solution. In the ordination plot, diets grouped by fish species and season (Fig. 4). Results from a two-way ANOSIM (species x season) indicated significant differences in diet for both species (R=0.633, p=0.001) and season (R=0.413, p=0.001). The greatest overlap in diet was between tule perch, bigscale logperch (R=0.292) and hitch (R=0.226) on the one hand, as well as inland silverside and yellowfin goby (R=0.237) on the other. SIMPER analyses indicated that inland silverside diet was strongly dissimilar to splittail (R=0.803) and carp (R=0.807). Splittail diet was in turn strongly dissimilar to threadfin shad (R=0.847), and carp diet was strongly dissimilar to delta smelt (R=0.856). Threadfin shad diet exhibited intermediate levels of dissimilarity to inland silverside (R=0.547) and delta smelt (R=0.536). Diets of inland silverside and delta smelt were only somewhat dissimilar (R=0.340).

A simple overlay of prey taxa onto the species and season NMDS plots showed prey groupings within the ordination (Fig. 5). SIMPER indicated that seasonal diet differences were due to larger contributions by amphipods (53 %) and copepods (17 %) in spring 2010, insects (61 %) and detritus (13 %) in summer 2011, and amphipods (41 %), cladocerans (17 %), and copepods (12 %) in winter 2012.

Discussion

Our results are some of the first to show how fish are foraging in shallow water habitat and indicate that the restoring tidal marsh at Liberty Island provides feeding habitat and prey resources for several fish species which are comparable to other wetlands, both restored and natural, throughout the San Francisco Estuary (SFE) and elsewhere (James-Pirri et al. 2001; Nemerson and Able 2005; Visintainer et al. 2006; Cohen and Bollens 2008). Differences in diet and prey biomass were observed across seasons, but far less so across sites, although this finding must be tempered by our limited sample size.

Although there was spatial overlap in the occurrence of fish species along the vegetation gradient (Whitley and Bollens, in review), potential resource competition may be reduced by the dietary partitioning of these co-occurring fishes. While our seasonal sampling occurred in three different years, there was some diet overlap in the prey taxa consumed across seasons, however the primary prey biomass was slightly different for each fish species. Seasonal shifts in diet most likely corresponded to changes in the availability of various prey. For example, the zooplankton communities in both open water (Kimmerer and Orsi 1996; Bollens et al. 2002, 2011) and intertidal marshes (Bollens et al. in review) of the San Francisco Estuary (SFE) exhibit seasonal shifts (e.g., *E. affinis* being dominant in the spring to *P. forbesi* being dominant during summer and autumn). Furthermore, extensive seasonal flooding may alter prey availability. Extensive flooding occurred in the Yolo Bypass in winter-spring 2011, which could have generated substantial chironomid production prior to our summer 2011 sampling event (Sommer et al. 2001a, b; Benigno and Sommer 2008).

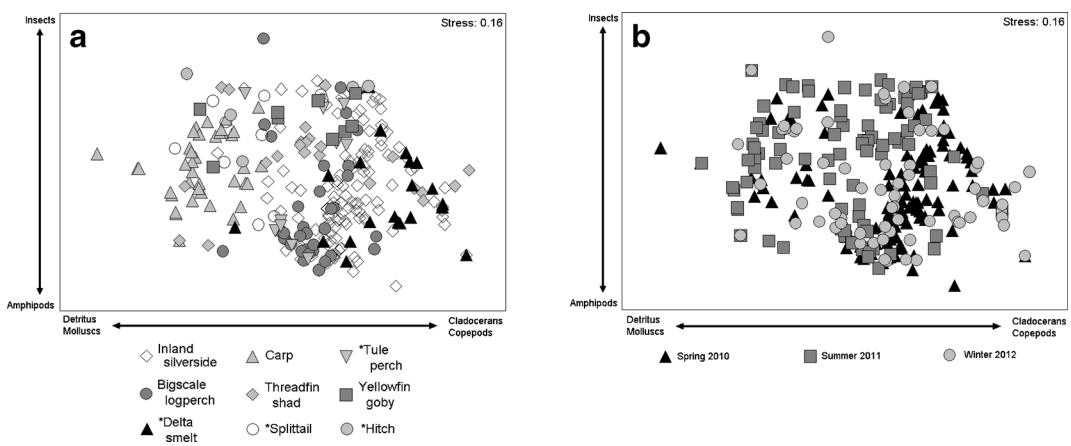

Fig. 4 Two-dimensional NMDS ordination plots of fish diets shown by (**a**) species and (**b**) season. *Indicates native fish species

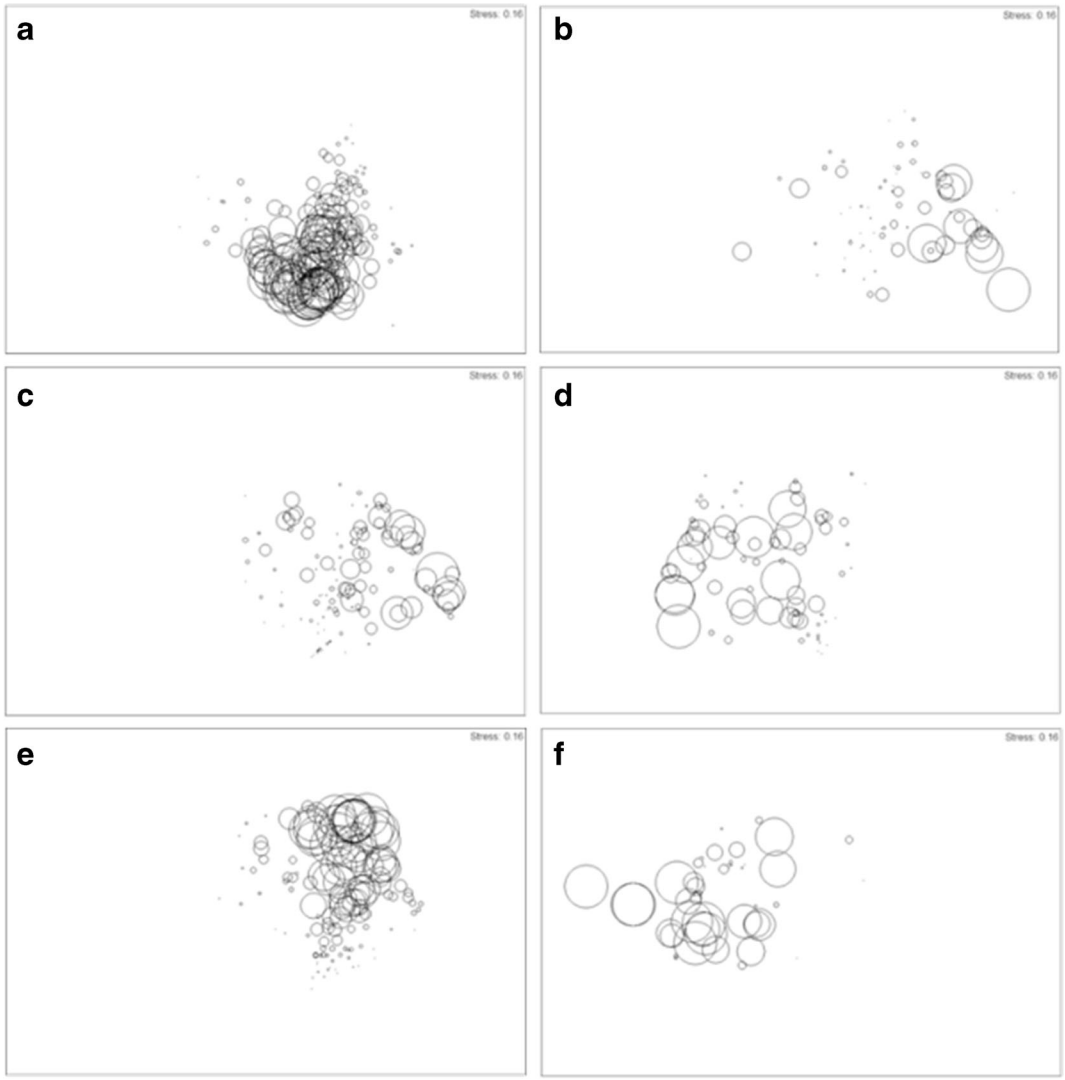

Fig. 5 Overlay of prey taxa onto NMDS ordination plots of Fig. 4. Larger *circles* indicate a greater proportion of prey taxa: (**a**) amphipods (**b**) cladocerans (**c**) copepods (**d**) detritus (**e**) insects (**f**) Mollusca

The importance of small fish in the diets of striped bass and white catfish increased substantially during summer. This increase in piscivory during the summer was likely due to an increase in abundance and availability of small-bodied fish at this time. Nobriga and Feyrer (2007) found that striped bass are typically more piscivorous during summer and autumn. Stevens (1966) found threadfin shad and smaller striped bass in the stomachs of adult striped bass from various regions within the Delta. We found no evidence of piscivory upon delta smelt, but instead we found that striped bass fed primarily on inland silverside (based on prey number) and largemouth bass and bigscale logperch (based on prey biomass). These periods of increased piscivory may lead to shorter foraging times and smaller foraging volumes for smaller fish, thus increasing competition among these smaller fish (Walters and Juanes 1993). Predator-encounter rates can be high in marshes during flood tide (McIvor and Odum 1988), however studies also confirm that marshes are important refuges from predation for small fishes (Boesch and Turner 1984; Halpin 2000).

We also found that striped bass consumed mysids mostly during spring, which aligns with other studies within the Delta that have found early juvenile striped bass feeding heavily on mysid shrimp year-round, but

especially during spring (Stevens 1966; Feyrer et al. 2003). Stevens (1966) found that when mysids were scarce during summer and autumn, *Corophium* sp. became an important prey item for young and juvenile striped bass. This is consistent with our findings of increased amphipod biomass, mostly *Corophium* sp., in the stomachs of striped bass during summer and winter. Furthermore, Bryant and Arnold (2007) found that juvenile striped bass diet consists of copepods, and that once these fish reach 50 mm in length, their diets shift towards an increase in amphipods and insects.

White catfish are known to be omnivorous both in their native range along the Atlantic coast (Menzel 1945; Heard 1975) and in the Delta (Turner 1966a). Turner (1966a) found that *Corophium* sp. and mysids were the most important food items for white catfish of all ages and that fish only occurred in about 3 % of stomachs. Our findings were similar in that white catfish consumed primarily *Corophium* sp., algae and other vegetation, as well as a small portion of fish.

Our findings of inland silverside diet composition are somewhat different than those found in previous studies in both their native habitats (Carr and Adams 1973) and in the lower SFE (Visintainer et al. 2006; Cohen and Bollens 2008). Inland silversides are often classified as opportunistic omnivores, feeding on copepods, amphipods, and insects (Darnell 1958; Weinstein 1986; Visintainer et al. 2006). This pattern is consistent with the seasonal dietary shifts observed in our study. However, we also observed a shift in prey across the vegetation gradient. In summer, inland silversides consumed primarily insects, except in the less vegetated habitat, where they consumed mostly sediment and crustacean parts. In spring, they consumed primarily amphipods, except in densely vegetated habitat, where they consumed mostly insects. Insects are widely known to be associated with vegetation (Batzer and Wissinger 1996; Tolonen et al. 2003), although chironomids are often associated with sediment (Benigno and Sommer 2008). The consumption of more amphipods in the spring in less densely vegetated habitat may be caused by a combination of low insect availability and greater amphipod availability. Previous studies have found that the amphipod distribution depends on many factors, including vegetation and substrate preferences of individual species (Van Dolah 1978). Our results on diet of inland silverside suggest that, in addition to the seasonal shifts, each site along the vegetation gradient may provide specific prey types of differing quality (Barry et al. 1996).

Delta smelt have been recorded to feed primarily on zooplankton, with some predation on mysid shrimp (Moyle et al. 1992; Lott 1998; Moyle 2002; Nobriga 2002; Hobbs et al. 2006). We found zooplankton was the primary prey source for delta smelt at Liberty Island, however larval insects during spring and amphipods during winter were also important prey items. Access to marsh habitats provides higher energy resources, such as chironomids (Gray et al. 2002, in review), which may prove beneficial for delta smelt growth, as seen with other species. For example, Halpin (2000) found that mummichogs (*Fundulus heteroclitus*) that had access to intertidal salt marshes in Rhode Island exhibited higher growth rates than those found in subtidal habitats. Similarly, Jeffres et al. (2008) found that Chinook salmon reared on ephemeral floodplains in California exhibited higher growth rates than those reared in perennial ponds or rivers. Sommer et al. (2001b) also found that chironomids enhanced Chinook salmon growth rates in Yolo Bypass. However, more specific studies are needed to determine if delta smelt exhibit increased growth rates with access to marsh habitats versus open water. For instance, delta smelt that utilize marsh habitat may consume a wider variety of prey, which could relieve potential resource competition, or alternatively, intensify competition with predominantly marsh-dwelling species such as inland silversides. Feyrer et al. (2003) studied dietary shifts in fish assemblages pre- and post-invasion of the overbite clam in the SFE and found that threadfin shad and delta smelt exhibited very similar diet composition, niche breadth and stomach fullness patterns, suggesting significant resource overlap. In our study, we did not find high diet overlap between delta smelt and any other species collected, but again, the relative importance of access to marsh versus open water habitats in modulating potential resource competition remains to be determined.

In the Delta, threadfin shad in all life stages are typically planktonic feeders (Turner 1966b; Feyrer et al. 2003). We found this to be true in our study, except during summer, when threadfin shad were more opportunistic, feeding on planktonic organisms, insects and small fish. Ingram and Ziebell (1983) found in a laboratory study that threadfin shad fed on chironomids when no other food was available, but that they would choose *Daphnia* sp. over the chironomids when

given a choice. Threadfin shad in our study seemed to be more opportunistic in response to prey availability during summer.

Diet of bigscale logperch within the Delta is undocumented. We found the primary prey taxa included amphipods (mostly *Corophium* sp.), insects (mostly chironomid larvae) and plant detritus. A close relative, the Texas logperch (*Percina carbonaria*), is classified as an insectivore, feeding mostly on insect larvae (Linam and Kleinsasser 1998).

Yellowfin goby diet composition in our study was slightly different than previous studies in their natural range (Japan) and elsewhere in the SFE. Kanou et al. (2004) studied food habits of fish on unvegetated tidal mudflats in Tokyo Bay and found that yellowfin gobies consumed plankton, amphipods, benthic crustaceans, and polychaetes, with the latter being an important diet component for adults. Similarly, Cohen and Bollens (2008) found that yellowfin goby diet composition in the Napa River system within the lower SFE consisted mostly of amphipods, polycheates, oligochaetes, harpacticoid copepods, cumaceans, and tanaids. Workman and Merz (2007) studied yellowfin gobies in California's Mokelumne River and found that chironomids made up the largest portion of the diet, with Gammarid amphipods being the next largest component. In our study, yellowfin goby diet consisted of insects, primarily chironomid larvae as well as Zygoptera nymphs (damselflies) in less vegetated habitat. Amphipods made up a very small percentage of the diet composition and we found very few benthic crustaceans. These findings suggest that yellowfin gobies have the ability to switch feeding modes in response to prey availability, making them successful invaders. It appears that in freshwater habitats, they consume mostly insects, while in more saline habitats they consume polycheates and benthic crustaceans.

The diet composition of the native tule perch has been documented to consist almost exclusively of amphipods (*Corophium* sp. and Gammaridae) (Feyrer et al. 2003). We also found that amphipods were an important diet component for tule perch. However, Zygoptera nymphs were also an important diet component in summer.

Splittail diet consists primarily of detritus and to a lesser degree, mollusks (Daniels and Moyle 1983), although earlier studies have shown that prior to the invasion of the overbite clam in the SFE in the late 1980's, mysids were an important non-detrital prey item (Feyrer et al. 2003). Similarly, we found splittail consumed primarily detritus, but we also found that splittail consumed some insects and a small portion of amphipods during winter. These additional winter food resources could provide more energy to prepare splittail for their spring spawning season.

There are no reported diet studies on the native hitch within the Delta. Geary and Moyle (1980) studied hitch in Clear Lake, California and found that smaller individuals (19–30 mm SL) primarily consumed chironomids, however as fish grew, *Daphnia* sp. became an important food item. They presumed adult hitch fed almost exclusively on *Daphnia* sp., as well as other zooplankton and adult midges. We found that sub-adult and adult hitch (150–213 mm FL) not only consumed sediment and detritus, but also a considerable proportion of insects (mostly Corixidae nymphs), suggesting that wetland habitat may provide hitch with a greater breadth of food resources.

Studies have found that diet of carp is based on detritus (Chapman and Fernando 1994; Garcia-Berthou 2001), which is similar to our findings, except that we found mollusks to be an important prey item during spring. Michel and Oberdorff (1995) found that chironomids and mollusks are the most important animal prey for carp.

Several studies have shown fish stomach fullness increases during tidal inundation of marshes, when fish gain access to marsh habitat (Rozas and LaSalle 1990; West and Zedler 2000; Laffaille et al. 2001; Hollingsworth and Connolly 2006). We found minimal differences in normalized stomach content weight across the vegetation gradient for any fish species, suggesting that fish are able to maintain stomach fullness throughout all sites. Our results are similar to other breeched-levee restoration studies (Nemerson and Able 2005; Cohen and Bollens 2008) in which overall prey quantity and availability seemed to allow most fish to feed in most wetland sites. However, Nobriga et al. (2005) found that nearshore habitats of Liberty Island had low fish biomass density compared to their other sites, suggesting Liberty Island was less productive than other nearshore locations in the Delta. Nevertheless, Lehman et al. (2010) found that Liberty Island was a potential large source of dissolved organic carbon that could support primary production, which then would provide good food resources for secondary producers and mesozooplankton, such as *Eurytemora affinis* and *Pseudodiaptomus forbesi*.

Liberty Island is notably different from other flooded islands in the central and south Delta. There is a fairly consistent influx of nutrient-rich water into Liberty Island from the adjacent sloughs and from tidal action, which may potentially enhance productivity (Lehman et al. 2010). Higher productivity may suggest that clams may not have as great an impact on the Liberty Island food web as in other flooded islands within the Delta (Lucas et al. 2002). The nearshore food web in other tidal wetlands within the Delta are supported largely by invertebrates grazing on the epiphytic macroalgae of submerged aquatic vegetation (SAV) (Grimaldo et al. 2009). We observed a higher seasonal abundance of SAV at Liberty Island during summer, although Nobriga et al. (2005) found that SAV abundance at Liberty Island is low compared to other Delta islands. Centrarchid fish that are typically associated with SAV (Grimaldo et al. 2004, 2012) were not collected in our study. The absence of piscivorous centrarchid fish at Liberty Island may promote the presence of native fish species.

Overall, it appears that fish utilizing marsh habitat at Liberty Island responded to seasonal changes by exploiting seasonally abundant prey and changing their diets to sustain stomach fullness and maintain minimal dietary overlap (Fig. 4). Although there were no significant diet differences across the vegetation gradient for most fish species, small differences in diet composition suggest that as vegetation succession continues, each vegetation type may provide specific habitat and prey resources. Our study demonstrates that prey resource use varies between seasons and across the vegetation gradient at Liberty Island and is generally species-specific; therefore restoration managers should consider species-specific needs for habitat and prey resources when planning and implementing tidal marsh restoration. More specifically, our results show that the endangered delta smelt will forage in tidal marsh habitats. Future studies should compare food webs between restoring tidal marshes and open-water habitats (e.g., open water habitats may be less complex and may have lower species diversity and a less complex food web in comparison to tidal marsh habitat). The diets of larval fishes, including the role of protistan prey (Bollens and Sanders 2004; Rollwagen-Bollens et al. 2011; Friedenberg et al. 2012), should also be considered in these future studies. Such comparative studies of shallow-water and open-water habitats will aid management in achieving the goal of creating conditions that optimize habitat quality for different species of native fishes.

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