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Trophic ecology and population attributes of two resident non-game fishes in riverine habitat engineered to enhance salmon spawning success

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Habitat enhancement efforts meant to improve conditions for fish in degraded rivers have the potential to impact all resident fishes — not just the focal population. Yet post-project ecological monitoring is often inadequately conducted, and in cases where restoration targets a single species, the impact on non-target fishes may be neglected. We investigated the diet and population attributes of two non-focal, resident fish species, the Sacramento pikeminnow (*Ptychocheilus grandis*) and prickly sculpin (*Cottus asper*), upstream of and within engineered habitat (hereafter the reference and restored reaches, respectively) intended to improve Chinook salmon (*Oncorhynchus tshawytscha*) spawning success. Population density, body size, stomach fullness, and prey importance were compared between populations residing in the reference and restored reaches. We also determined if the primary carbon source that supported common pikeminnow and sculpin prey differed between reaches using stable isotope analysis. Pikeminnow residing in the restored reach were significantly larger but less densely populated, exhibited greater condition factor values, and consumed more large-bodied prey. In contrast, sculpin in the restored reach were significantly smaller and more densely populated relative to the reference reach. Analysis of isotopic signatures suggests that macroinvertebrates supporting fish populations as prey principally depend on diatomaceous algae in the restored habitat, while filamentous algae were most important in the reference reach. Results suggest that restored salmonid habitat may represent significantly different environmental settings for non-target fish species, with consequences for population structure and diet.

Key words: Chinook salmon, *Cottus asper*, food web, gravel augmentation, Merced River, *Oncorhynchus tshawytcha*, prickly sculpin, *Ptychocheilus grandis*, Sacramento pikeminnow

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The effects of most common habitat rehabilitation practices on many fish species remain poorly understood. More than US $15 billion has been spent on stream and river restoration in the United States over the past twenty years (Bernhardt et al. 2005, Bernhardt et al. 2007). Unfortunately, a majority of project ecosystems are not adequately monitored once completed (Bash and Ryan 2002, Jansson et al. 2005, Bernhardt et al. 2007). In cases where restoration efforts are meant to improve conditions for a single focal species, post-project monitoring of non-target fish populations is often altogether absent. Yet, many habitat augmentation projects have considerable potential to influence various ecosystem components, including non-target resident fish species. For example, installing structures to improve habitat for stream-dwelling salmonids may increase organic matter retention (Rosi-Marshall et al. 2006), induce shifts in macroinvertebrate community dynamics (Merz and Chan 2005), and alter the abundance of key primary producers (Muotka and Syrjanen 2007), while in other cases biological metrics may be little affected by restoration efforts (Jahnig et al. 2009, 2010). Regardless of the outcome of restoration on target species, restructuring aquatic habitats may affect most any population of resident stream fishes by altering the food web. Given the growing popularity of habitat restoration as a fundamental management approach and high proportion of freshwater ichthyofauna at risk of extinction (Jelks et al. 2008), there is a need to develop a more holistic understanding of how standard restoration techniques affect all resident species.

In the Central Valley region of California, numerous stream and river restoration projects have been implemented in response to acute environmental degradation. Most Central Valley river ecosystems have been altered by dams, water diversions, historic and modern mining, introduced flora and fauna, and nutrient enrichment (Yoshiyama et al. 1998, Moyle et al. 2003, Brown and Bauer 2010). Management actions associated with river restoration in the region have overwhelmingly involved attempts to improve spawning and rearing conditions for Chinook salmon (*Oncorhynchus tshawytscha*), a species whose adult spawning populations within the Central Valley reached historic lows in 2009. The effects of restoration efforts targeting salmon recovery on non-target fishes and ecosystem processes are not well understood even though they have the potential to be extensive. Salmon spawning habitat restoration often involves whole-channel realignment, substrate alteration, the installation of structural complexity, or the adjustment of flow regimes (Flosi et al. 1998, Roni et al. 2002). Such actions may fundamentally alter habitat, affect holistic ecosystem properties such as temperature and flow, and induce shifts in food web structure. Thus, spawning habitat restoration is likely to affect all resident fishes. A significant proportion of Central Valley ichthyofauna and river-dependent herpetofauna are threatened or in decline (Fisher and Shaffer 1996, Moyle 2002), heightening the need for thorough post-project assessment that includes non-target species.

One such effort to restore salmon populations through habitat manipulation is the Merced River Salmon Habitat Enhancement Project (MRSHEP), which involved complete channel realignment and gravel augmentation in a 2.7 km river reach (Marshall et al. 2008). Physical habitat attributes potentially important to many resident fishes vary between the MRSHEP reach and unenhanced habitat. The engineered reach possesses lower concentrations of fine sediments, less riparian shading, fewer pieces of large woody debris, and greater flow velocities. Post-project assessments of biological attributes suggest that attributes of the food web differ between reaches as well: Albertson et al. (2011) reported that the community in unenhanced habitat was dominated by the large, sessile, filter-feeding caddisfly (*Hydropsyche*) while a smaller, more mobile grazing mayfly (*Baetis*) was dominant in the restored reach. Overall invertebrate biomass was also lower in the restored reach (Albertson et al. 2011). These results suggested that differences in abundance between reaches could exist at higher trophic levels, as benthic macroinvertebrates are a principal diet component of many resident fishes.

We evaluated the population attributes and trophic ecology of two fishes collected within and outside of the MRSHEP reach to assess how the engineered channel supported populations of non-target resident species. Because the habitat template in the engineered channel is relatively distinct, we tested the hypothesis that the abundance, size structure, and condition factor of prickly sculpin (*Cottus asper*) and Sacramento pikeminnow (*Ptychocheilus grandis*) differed between the restored reach and locations upstream. In light of the disparity in macroinvertebrate abundance between the MRSHEP reach and locations upstream (Albertson et al. 2011), we also quantified the diet composition of both species to compare between restored and reference habitat. Finally, we used stable isotope analysis to determine if the macroinvertebrate taxa these fish depend upon as prey were reliant on variable sources of primary producers between restored and reference habitat. Our analyses are therefore meant to determine if differences in basic population attributes and trophic ecology for the two species of fishes fundamentally differ between restored and reference habitat in the Merced River and quantify such differences where they exist.

Materials and Methods

Study site.— The Merced River drains approximately 33,000 km^2 of land in the Sierra Nevada and Central Valley region of California (Figure 1). Watershed land cover includes primarily forest in the headwaters and upstream reaches and agricultural dominance downstream. As is typical of most Central Valley rivers in California, discharge is driven by snowmelt, although the modern flow regime is heavily regulated by a series of dams in the foothills of the Sierra Nevada. Multiple efforts have attempted to restore instream physical habitat in the Merced River with the goal of stabilizing and increasing the fall-run Chinook salmon stock (Kondolf et al. 1996, Marshall et al. 2008).

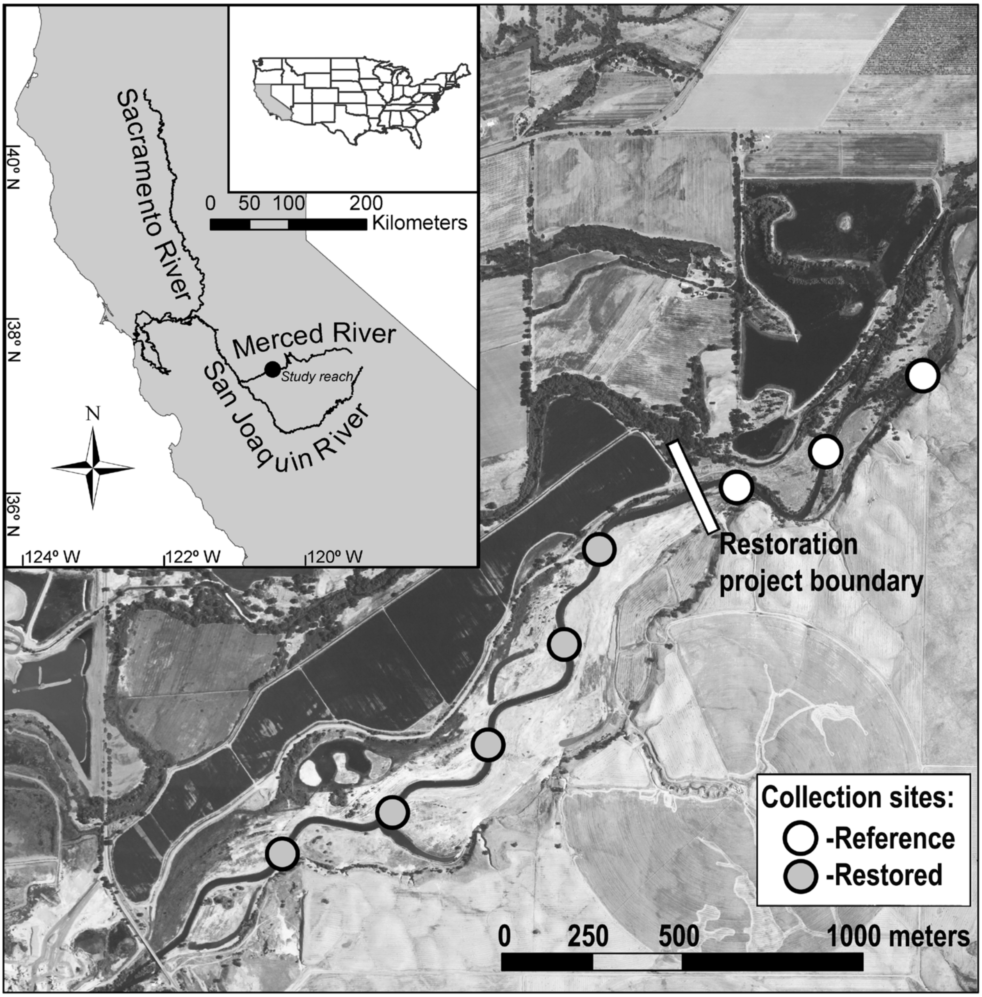

FIGURE 1.— Aerial imagery of the Merced River, Merced County, California and study site locations. Imagery was recorded during 2005.

To date, the largest among the restoration efforts in the Merced River is the MRSHEP. During the winter of 1997, a flood event resulted in levee failure that redirected all flow to an area formerly mined for gravel, creating a 2.7 km reach of broad, shallow, occasionally ponded and braided habitat (CDWR 2001). The MRSHEP project sought to convert this reach to habitat conducive for Chinook salmon spawning. Attributes of the project included the construction of a single channel with 10 pool-riffle sequences and subsequent addition of 1.5 million metric tons of coarse gravel. Completed in 2001, the project was designed to allow geomorphic processes such as point bar evolution, pool and riffle formation, and sediment transport to ensue under the modern flow regime. Although the MRSHEP was uniquely designed for the Merced River, restoration strategies involved in the project (such as channel realignment and gravel augmentation) are commonly applied in degraded Central Valley rivers (Kondolf 1998, Merz and Setka 2004, Marshall et al. 2008).

A "BACI" (before/after, control/impact; Krebs 1999) design would have been optimal to explicitly gauge the influence of restoration on the food web structure in the channel altered by the MRSHEP project (Baldigo 2010, Miller et al. 2010). However, as is true of most restoration efforts, the collection of biological data prior to project completion was not included in the MRSHEP design. Given this, we decided that the second best option was to compare the MRSHEP reach to an upstream site that had the same species pool, but which was not altered in any way by the restoration effort. We quantified the trophic attributes of non-target resident fishes, measured fish diets, population attributes and food web structure, and compared these between the MRSHEP reach and unenhanced habitat immediately upstream. We sampled multiple locations within the restored reach and in locations ≤1.7 km directly above the MRSHEP boundary (hereafter the restored and reference reaches).

Many physical habitat attributes vary between reaches. Table 1 lists reach-specific habitat parameters derived from a field-validated hydrogeomorphic model of the Merced River (Harrison et al. 2011) or collected for a related study (Albertson et al. *in press*) during the summer of 2008. The reference reach is slightly steeper, wider, and shallower than the restored reach. Pools are the dominant habitat unit in the restored reach, while runs dominate the reference reach. Because the channel is approximately 20% narrower but conveys the same discharge as the restored reach, average current velocity is greater in the MRSHEP reach. Sediments are more embedded and compacted (measured following Downes et al.

Table 1.— Physical habitat attributes compared between the restored and reference reaches of the Merced River, Merced County, California, 2007-2010. Data sources are indicated by superscripts 1 (Harrison et al. [2011]) or 2 (Albertson et al. [in press]).

Variable	Method(data source)	Reference	Restored
Slope ($\times10^{-3}$)	Comprehensive survey of both reaches[1]	2.6	2.5
Proportion of pool:riffle:run (by area)	Comprehensive survey of both reaches[1]	0.15/0.31/0.54	0.39/0.24/0.37
Bankfull width (m)	Mean from 1 m interval transects[1]	35.3	29.2
Wetted width (m)*	Mean from 1 m interval transects[1]	24.9	19.8
Mean depth (m)*	Mean from 1×1 m grid[1]	0.6	0.5
Mean velocity (m s^{-1})*	Mean from 1×1 m grid[1]	0.4	0.6
Embeddedness (%)	Following Bain (1999), two grids assessed per reach[2]	6.3	0.5
Compactedness (N)	Following Downes et al. (1997), two measurements per reach[2]	24.0	20.3
Median particle size (cm)	Two 100-sample pebble counts per reach[2]	6.4	5.7
Undercut banks (% of surveyed length)	Measured along 1 500m section per reach[2]	4.7	0.0
Wood density (n pieces per 100 m^{-2})	Measured within wetted channel of 1 500 m section per reach[2]	5.0	0.2
Mean wood volume ($\times10^{-2}$ m^{-3})	Derived from length and width of all pieces in 500 m section per reach[2]	1.5	0.7
Shade cover (%)	Standard spherical densiometer readings every 25 m in 500 meter sections, taken 1 m from bank[2]	32.0	0.2

*-values at standard baseflow (6.4 m^3 s^{-1}; CDWR 2011

1997) in the reference reach, largely due to elevated concentrations of fine sediment (Albertson et al. *in press*). Large woody debris is more abundant and consists of larger pieces (by volume) in the reference reach. The riparian zone throughout the study area is likely less extensive in comparison to conditions prior to agricultural expansion in the Central Valley (Hunter et al. 1999). However, deciduous trees are present in the reference reach whereas little vegetation other than grasses and shrubs have become established in the restored reach riparian area that was cleared during the construction period. Riparian shading is, therefore, two orders of magnitude lower in the restored reach relative to the reference reach (Table 1). Nevertheless, the lack of riparian cover apparently does not much increase conductive warming in the restored reach: the gain in mean daily temperature during September and October (both months are typically warm with low cloud-cover in the region) 2008 between the uppermost reference site and lowermost restored site was 0.2 °C. A minority of attributes, such as mean channel depth and median particle size, are similar throughout the study area.

Focal species.— Two native resident fish species were selected for detailed analysis based on their distinct habitat affinities in the Merced River. Both fishes are relatively abundant among the resident ichthyofauna. The Sacramento pikeminnow is a large-bodied cyprinid that inhabits the water column. Although adult pikeminnow are piscivores, the Merced River population is composed mostly of juveniles (< 150 mm) that usually consume benthic macroinvertebrates such as aquatic insects (Brown 1990, Nobriga et al. 2006). The prickly sculpin is a cryptic species that resides in benthos of both high and low velocity areas. Diet surveys have indicated that the prickly sculpin is principally an invertivore that specializes on aquatic insect larvae but will opportunistically capture small fish (Brown et al. 1995, Merz 2002, Moyle 2002).

Sample collection and processing.— Seine sampling and snorkel surveys were conducted during 5–9 August 2008 to estimate fish densities and collect individuals for diet and stable isotope analyses. To estimate sculpin abundance, we used a 2 × 2 m seine to survey three riffles in the reference reach and five in the restored reach (Figure 1). We sampled two fewer riffles in the reference reach because the next closest riffle was a large distance upstream and we wished to collect individuals from unenhanced habitat as close to the MRSHEP reach as possible. Two samplers held either side of the seine while two others rapidly turned over substrate in a 2 × 2 m area upstream of the seine to dislodge sculpin from the benthos. The seine was bailed after approximately 10 seconds and captured sculpin were enumerated. Pikeminnow are easily visible in the water column. Therefore, pikeminnow abundances were estimated using snorkel surveys. Three or four divers (depending on channel width) floated the entire length of each study reach and recorded fish counts. We collected pikeminnow for size (which was not estimated during snorkel surveys), condition factor, and diet analyses from pools downstream of the riffles where sculpin were sampled using a 10-m beach seine. All collected fish were frozen on-site with a portable freezer.

Stable isotope analysis was employed to determine dietary source contributions of primary producers to macroinvertebrate taxa that were dominant in the benthic community and diets of fishes. Samples of primary producers and invertebrates were collected for stable isotope analysis from the three riffle-pool sequences in the reference reach and five sequences in the restored reach during the same period in which fish sampling was conducted. Three replicate samples of all targeted food web components were collected from each of the sampled pool-riffle sequences and subsequently pooled prior to processing. Primary production sources included riparian grasses and deciduous trees, fine transported organic matter (FTOM), filamentous algae (primarily patches of *Cladophora*), and algae attached to substrate particles (hereafter benthic algae). Samples of live leaves and grasses were collected from three randomly selected areas in the riparian zone ≤3 m from the bank of each riffle-pool sequence. FTOM samples were amassed by passing whole water samples through a series of sieves to exclude particles >1,000 µm and <100 µm until material had visibly collected on the 100 µm sieve screen. Clumps of filamentous algae were located at each site and collected by hand. Samples of benthic algae were collected from ~50-mm rocks using a knife blade after first removing any visible consumer organisms. Benthic macroinvertebrates were collected using a 1-m kicknet with 500-µm mesh. All samples were placed in individual plastic bags and frozen on-site.

Our analyses were conducted exclusively during the summer of 2008 and are therefore temporally limited. The likelihood of disturbing embryonic or juvenile Chinook salmon and the flow pulses typically applied during the fall, winter, and spring by water project operators restricted the temporal extent of our study. We chose to conduct our work during the summer as that is the metabolically most important period (due to relatively elevated temperatures) for organisms in the Merced River. The Merced Irrigation District holds discharge in the lower Merced at a near-uniform level from late spring through early fall (CDWR 2011) and typical weather conditions (little to no precipitation, sparse cloud cover and warm temperatures) are consistently homogeneous during this period. Therefore, environmental conditions during the study sampling period were representative of a large proportion of a typical year. Regardless, our results should be viewed in the context of the study time frame, as annual events such as flood pulses (Bayley 1991) and nutrient inputs from salmon carcasses (Cederholm et al. 1999) that occur in seasons outside of our study time frame are likely to affect variables that we quantified.

Laboratory procedures.— Each fish was defrosted, measured to the nearest millimeter standard length (SL) and weighed to the nearest 0.01 g. Sculpin anterior digestive tracts were removed and each prey item was identified to the lowest feasible taxonomic level (typically genus) under a dissecting microscope. Pikeminnow do not possess a true stomach. Thus, pikeminnow contents from the entire digestive tract were identified and tallied. We converted prey item counts to estimated dry mass using mean taxon-specific biomass. Conversion to biomass was achieved by multiplying invertebrate counts by the mean taxon-specific dry mass of individuals collected from benthic kick samples obtained in a concurrent study (Albertson et al. 2011). Cumulative stomach contents for each fish were placed in individual tins and oven-dried at 60 ºC for 48 h to provide estimates of total stomach content dry mass once all prey items had been identified.

Fish tissue and other collections were prepared for stable isotope analysis. Subsamples of 18 fish per species (nine from each study reach) were selected to assess stable isotope composition. Pure samples of white muscle tissue were excised with a scalpel, rinsed with deionized water to remove scale and bone fragments, oven-dried at 60 ºC for 48 h, and ground with a mortar and pestle in preparation for isotopic analysis. Samples of FTOM and benthic algae were defrosted, centrifuged with colloidal silica solution to separate organic and detritus fractions (Hamilton et al. 2005) and filtered onto precombusted Whatman glass fiber filters. Defrosted leaves and grasses were rinsed with deionized water to remove foreign material. We selected two taxa of benthic macroinvertebrates, *Baetis* mayflies and *Hydropsyche* caddisflies, for stable isotope analysis aimed at determining if consumers were dependent on disparate primary producers between reaches. These two genera were specifically selected because they are numerically dominant (>50% by count) in the invertebrate assemblage of the restored and reference reaches, respectively (Albertson et al. 2011) and preliminary analyses suggested that both were important prey for resident fishes. All samples were subsequently dried in individually labeled tins at 60 °C for 48 hours and homogenized with a mortar and pestle (the latter step was not performed for filtered materials). Dried invertebrates were acidified to remove inorganic carbonates in the exoskeleton using the drop-by-drop method described by Ng et al. (2007) and re-dried prior to homogenization. Sub-samples of ground material (or whole filters) were pressed into tin capsules and sent to the Marine Sciences Institute Analytical Lab at the University of California, Santa Barbara for analyses of $\delta^{13}C$ and $\delta^{15}N$ values.

Data analysis.— We compared metrics that quantified fish density, body size, and condition factor between restored and reference reaches. Fish counts were converted to density estimates by dividing the numbers by area of habitat surveyed (for pikeminnow) or area of disturbed substrate (for sculpin). Differences in fish size between reaches were determined using standard lengths and the presence of multiple size-classes was detected using Hartigan's test for unimodality (Hartigan and Hartigan 1985). Condition factors (weight in g $\times$10,000 / [length in mm]^3) were calculated for both species and statistical analyses were split among classes if size distributions were polymodal to ensure that similar-sized fish were compared (Anderson et al. 1996). All aforementioned comparisons were performed with a Student's t-test with the exception of fish density, for which a Wilcoxon-Mann-Whitney rank sums test (Hollander and Wolfe 1999) was conducted due to the highly non-normal distribution of the data.

Diet data were assessed using a mix of univariate and multivariate procedures. The index of relative fullness was calculated (Herbold 1986) to quantify total prey consumption. To calculate this metric, the maximum potential stomach content mass for each fish was approximated by fitting a curve between maximum observed stomach content mass values (delineated by size classes) and fish length. Percent stomach fullness was then determined by dividing the observed mass by the estimated maximum potential mass based on fish size and compared between reaches using Student's *t*-test. Multivariate statistical procedures were performed on prey item-specific dry mass data to test for differences in diet composition between reaches. Diet data were relativized by prey category prior to multivariate analysis. Analyses of similarity (ANOSIM; Clarke 1993) tests were conducted to determine if overall diet composition differed significantly between reaches, and indicator species analysis (ISA; Dufrene and Legendre 1997) subsequently identified prey items that were disproportionately consumed in each reach. We also constructed diet composition biplots (Amundsen et al. 1996) to illustrate trends in prey importance. To construct these plots, the mean prey item frequency of occurrence among fish is placed on the x-axis and proportion of total mass the prey item represented when present in a stomach is represented on the y-axis. These biplots allow visual assessment of predator niche breadth and degree of specialization: if prey items are in the upper-right hand corner of the plot, predators are considered specialists on those prey while an agglomeration of points near the lower-left hand corner suggests that predators adopt a generalist strategy (Amundsen et al. 1996).

Stable isotope data were used to estimate which primary producers were most important in supporting key consumer taxa and if the two focal fish species were feeding at different trophic levels between reaches. We used MixSIR version 1.0.4 (Moore and Semmens 2008) to determine the relative contribution of autochthonous and allochthonous primary production sources (deciduous trees, riparian grasses, benthic algae and FTOM) that support *Baetis* and *Hydropsyche*. MixSIR uses a Bayesian framework to estimate probability distributions of the contribution of multiple sources (primary producers) to a mixture (consumers) using stable isotope values. The approach provides advantages over other mixing models by accounting for variability in the observed isotope ratios of consumers and sources as well as uncertainty in diet-tissue fractionation. Means and standard deviations of diet-tissue fractionation for consumers were drawn from Jardine et al. (2005). Finally, we used $\delta^{15}N$ values to determine if fish in the two reaches were feeding at different trophic positions (Post 2002). Following the methodology of Cabana and Rasmussen (1996), the trophic position of pikeminnow and sculpin each was derived using the equation:

$$TP = [(\delta N^{15}\text{ fish tissue} - \delta N^{15}\ \textit{Baetis}) / 3.4] + 2$$

where TP= trophic position, $\delta^{15}N$ *Baetis* is the pooled local (restored or reference) mean of *Baetis* larvae, and 3.4 represents the fractionation of δN^{15} between fish and their prey. *Baetis* was chosen as a baseline-correcting primary consumer because it was ubiquitously found in the stomachs of both species and the taxon is numerically dominant in the macroinvertebrate community, particularly in the restored reach (Albertson et al. *in press*).

All parametric, non-parametric, and ANOSIM model tests were performed in R version 2.11.0 (The R Foundation for Statistical Computing 2011). ISA was conducted using PCOrd version 2.10 (McCune and Medford 2006).

Results

Numerous attributes of Sacramento pikeminnow and prickly sculpin differed significantly between the restored and reference reaches (Table 2). Pikeminnow were more densely populated (W= 2398, P<0.01) and significantly smaller (t=4.0, P<0.01) in the reference reach, while sculpin density was greater (W= 68, P<0.01) but individuals were significantly smaller (t=5.4, P<0.01) in the restored reach. Both populations exhibited polymodal size distributions (Hartigan's test for unimodality P-value <0.05; Figure 2), suggesting that multiple cohorts were represented in the population for both species.

Table 2.— Attributes of Sacramento pikeminnow and prickly sculpin between restored and reference reaches of the Merced River, Merced County, California, July-August 2008. Shown are means ±1 standard error. Bold type represent values that were statistically different (P <0.05) between reaches when compared with a Student's t-test except for estimates of density, which were compared using a Wilcoxon-Mann-Whitney rank sums test.

		Reach	
Fish species	Variable	Reference	Restored
Sacramento pikeminnow			
	Density (n $m^{-2}\times10^{-2}$)	**5.0±1.4**	**1.2±0.2**
	Length (mm)	**79.2±2.3**	**91.7±2.1**
	Condition factor, fish <80 mm	**1.7±0.0**	**1.9±0.1**
	Condition factor, fish >80 mm	1.6±0.1	1.7±0.1
	Stomach fullness (%)	**35.6±2.4**	**43.6±3.0**
	Trophic position	3.3±0.1	3.3±0.1
Prickly sculpin			
	Density (n $m^{-2}\times10^{-1}$)	**0.7±0.2**	**1.9±0.4**
	Length (mm)	**67.8±2.4**	**51.2±1.9**
	Condition factor, fish >40 mm	2.3±0.1	2.2±0.1
	Stomach fullness (%)	37.9±3.5	46.7±4.2
	Trophic position	3.2±0.1	3.3±0.1

Pikeminnow condition factor values were significantly higher in the restored reach for fish less than or equal to 80 mm (t=2.6, P<0.05), although no such difference was detected between reaches in the greater than the 80-mm size class (t=0.4, P=0.69). Analysis of condition factors for sculpin was restricted to individuals greater than 40 mm due to an absence of small fish in the reference reach. For this size group, means between reaches did not significantly differ (t=1.5, P=0.13). Pikeminnow (t=2.1, P<0.05), but not sculpin (t=1.6, P=0.11), stomach fullness estimates were significantly greater in the restored reach.

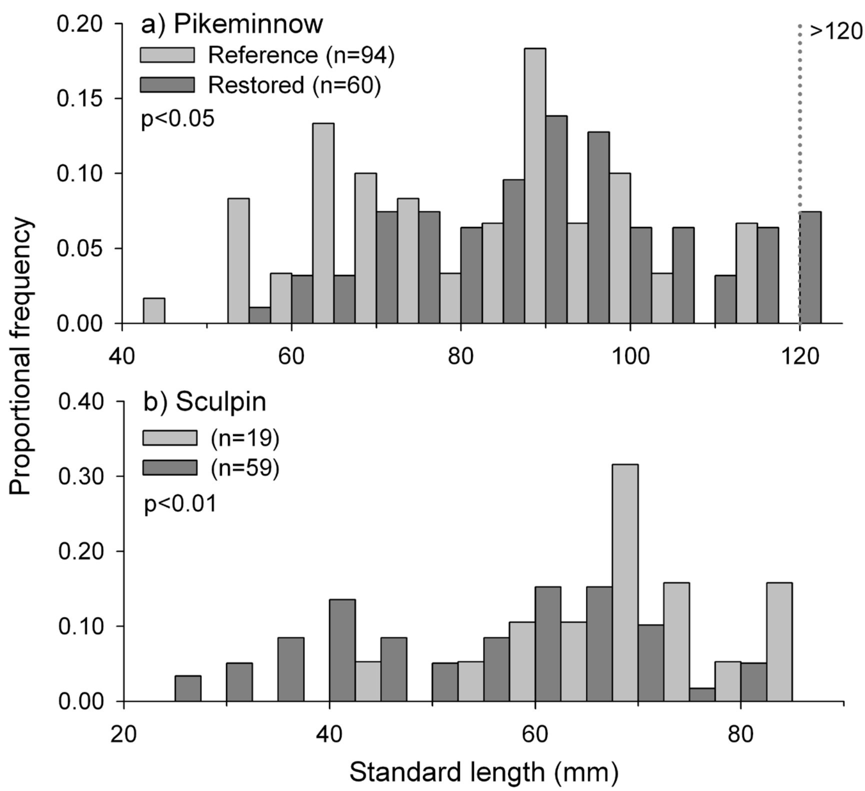

Figure 2.— Length-frequency histograms of (a) Sacramento pikeminnow and (b) prickly sculpin collected in the restored and reference reaches of the Merced River, Merced County, California, 5-9 August 2008. P-values for Hartigan's dip test of unimodality are provided.

ANOSIM models suggested that overall diet composition differed significantly between reaches for pikeminnow (P<0.05, R=0.05) but not sculpin (P=0.20, R=0.06). Although 14 taxa were found in pikeminnow stomachs, five prey categories (the mayfly *Baetis*, caddisfly *Ceraclea*, fish, gastropods, and caddisfly *Hydropsyche*) constituted more than 90% of the total diet by mass. ISA suggested that reference reach pikeminnow consumed significantly more *Ceraclea* (*indicator value* [*IV*]=53.0, P<0.01) and *Hydropsyche* (*IV*=45.2, *P*<0.05), while restored reach diets were characterized by gastropods (*IV*=36.7, *P*<0.01) and small fish (*IV*=15.1, *P*<0.01). Only restored-reach pikeminnow consumed earthworms and fish, the latter of which were likely western mosquitofish (*Gambusia affinis*), though a positive identification was not possible. Ten taxa were identified among sculpin stomachs, three of which (*Baetis* and caddisflies *Culoptera* and *Hydropsyche*) represented more than 95% of all diet by mass. One relatively minor prey taxon, the mayfly *Heptagenia*, had a statistically significant indicator value (*IV*=30.1, *P*<0.05; elevated consumption in the restored reach). The consistent position of caddisflies (especially *Hydropsyche*) in sculpin prey biplots (Figure 3) suggested that sculpin are prey specialists in both reaches. In contrast, the absence of prey items in the upper-right quadrant of pikeminnow diet biplots (Figure 4) suggests this species adopts a more generalist feeding pattern and relies on a more diverse suite of prey items. Stable isotope analyses suggested that neither assessed fish species appeared to be feeding at different trophic positions between reaches. Trophic position estimates did not differ significantly between reaches for pikeminnow (*t*=0.8, *P*=0.44) and sculpin (*t*=1.1, *P*=0.29).

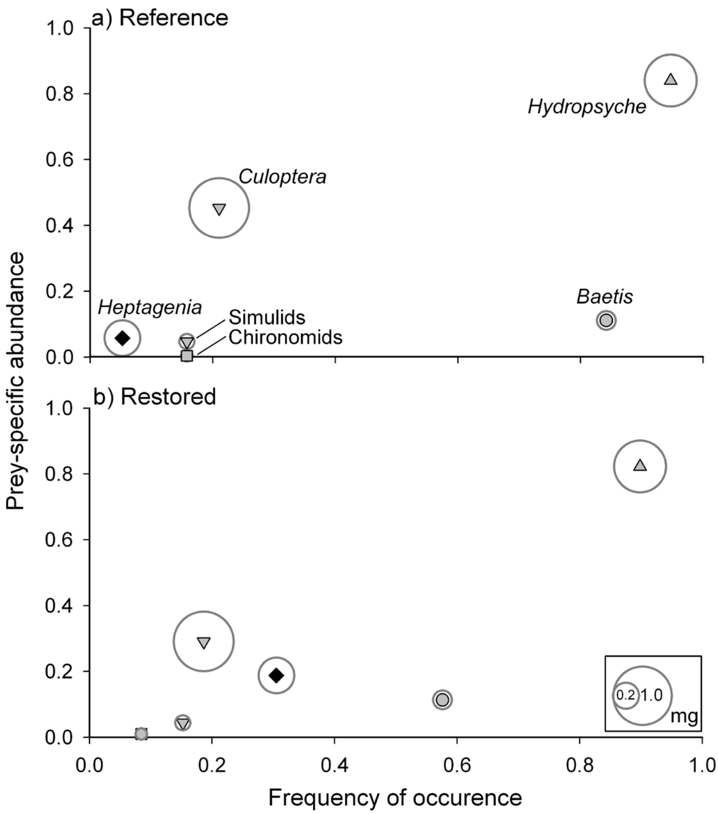

Figure 3.— Specific abundance and relative frequency biplots (Amundsen et al. 1996) of prey consumed by prickly sculpin in the (a) reference and (b) restored sections of the Merced River, Merced County, California, 5-9 August 2008. Prey-specific abundance refers to the proportion of the total diet a prey class represented (by mass) when present in a stomach; frequency of occurrence represents the proportion of fish collected with the corresponding prey class. Only items present in ≥5% of fish in either section are shown. Black symbols represent significantly different indicator prey between reaches. Circles surrounding each point denote the mean dry mass (mg) of each prey item.

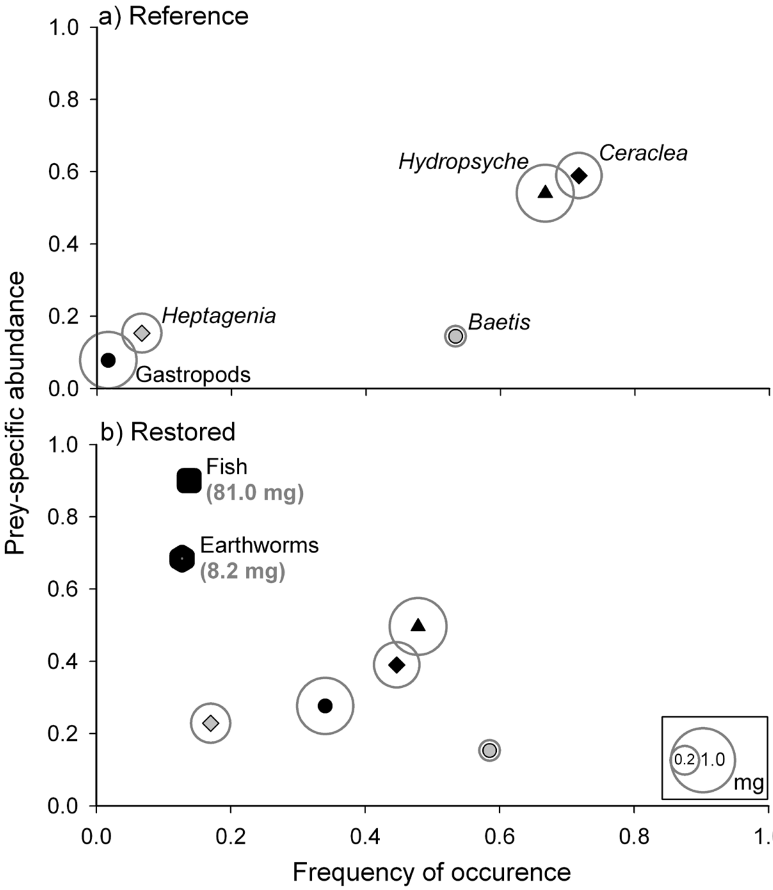

Figure 4.— Specific abundance and relative frequency biplots (Amundsen et al. 1996) of prey consumed by Sacramento pikeminnow in the (a) reference and (b) restored sections of the Merced River, Merced County, California, 5-9 August 2008. Prey-specific abundance refers to the proportion of the total diet a prey class represented (by mass) when present in a stomach; frequency of occurrence represents the proportion of fish collected with the corresponding prey class. Only items present in ≥5% of fish in either section are shown. Black symbols represent significantly different indicator prey between reaches. Circles surrounding each point denote the mean dry mass (mg) of each prey item. Dry mass circles are not shown for fish and earthworms (represented by enlarged symbols), as these prey were excessively large.

Mixed-source Bayesian models of $\delta^{13}C$ and $\delta^{15}N$ data suggested that the *Baetis* and *Hydropsyche*, both of which are key sculpin and pikeminnow prey taxa, derived carbon from different primary production sources between reaches (Figures 5 and 6). Between reaches, the relative contribution of specific autochthonous primary production sources to *Baetis* and *Hydropsyche* varied (Figure 6). Model results suggested that *Hydropsyche* derived energy from either filamentous or benthic algae, or both (the degree of uncertainty associated with each was considerable), with a relatively minor contribution from FTOM in the reference

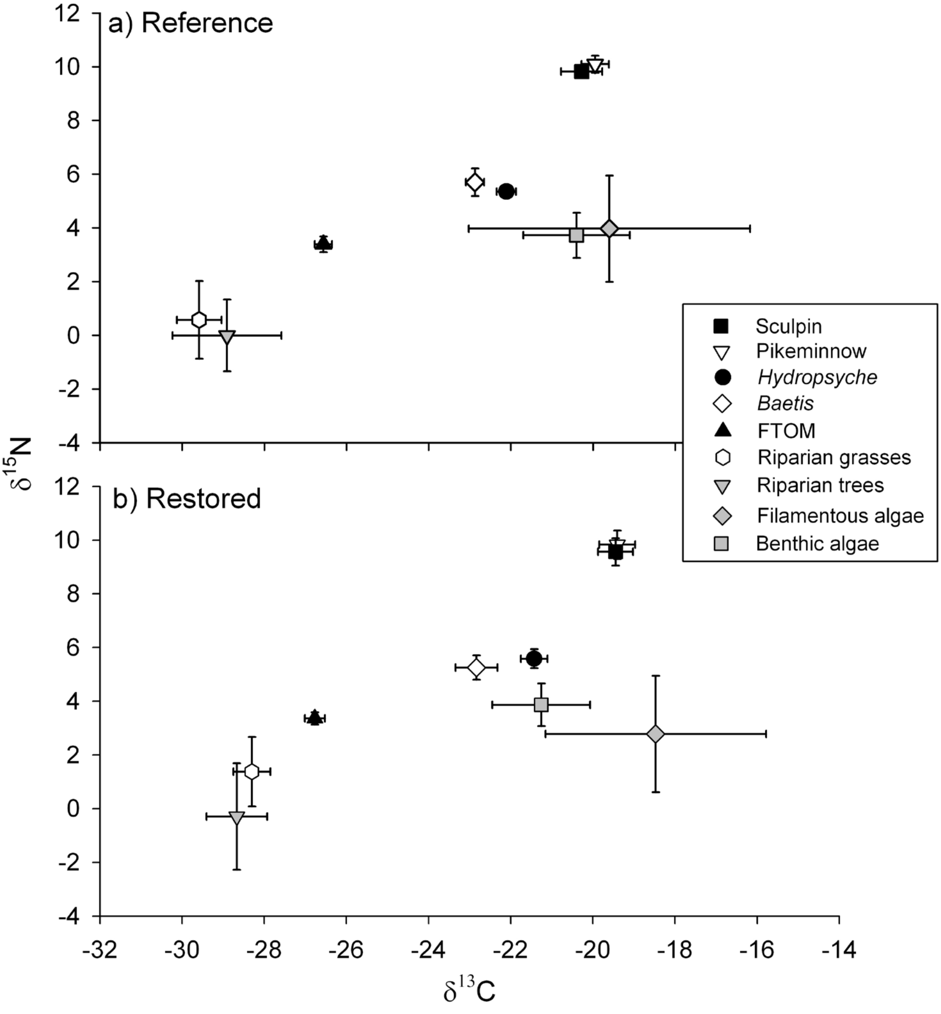

Figure 5.— $\delta^{13}C$ and $\delta^{15}N$ biplot of food web components between the (a) reference and (b) restored reaches of the Merced River, Merced County, California, 5-9 August 2008. Shown are mean values ±95% confidence intervals.

reach. Within the restored reach, however, *Hydropsyche* derived a majority of carbon from a benthic algae source and the degree of contribution from filamentous algae and FTOM diminished. Reference reach *Baetis* relied primarily on filamentous algae as a carbon source, with benthic algae and FTOM of secondary and tertiary importance, respectively. In contrast, restored reach *Baetis* relied primarily on benthic algae, while the relative importance of filamentous algae was reduced and the role of FTOM remained similar to the estimated contributions in the reference reach.

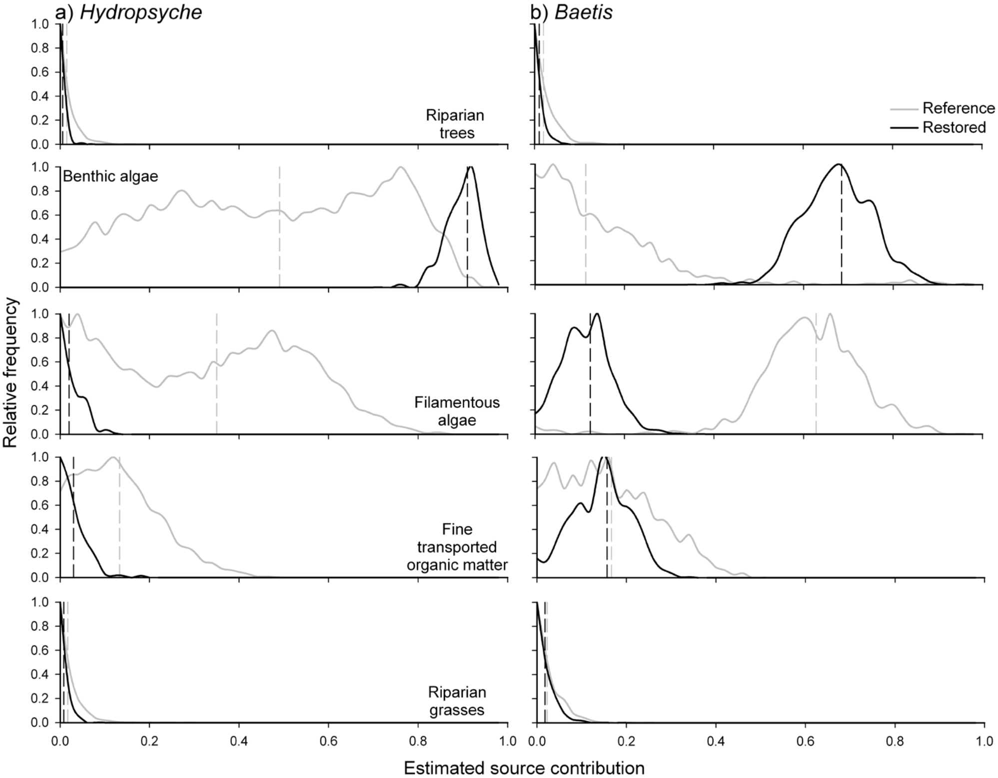

Figure 6.— Distribution of estimated primary producer source contribution values to (a) Hydropsyche and (b) Baetis biomass between reference and restored reaches of the Merced River, Merced County, California, 5-9 August 2008. Shown are the frequencies of source contribution estimates (derived from 10,000 iterations) relative to the maximum (i.e., the modal source contribution estimate possesses a value of 1). Dashed lines represent the median source contribution among estimates for each distribution.

Discussion

Our results suggest that a channel engineered to promote salmon passage and spawning provided a disparate, but suitable, environment for non-target fish species relative to unenhanced habitat in the Merced River. Stomach fullness and condition factor values suggest that the MRSHEP represents improved conditions for small (<80 mm) Sacramento pikeminnow relative to reference habitats upstream, although the restored reach supported reduced densities. Such effects appear to have been driven partly by dietary shifts: restored-reach pikeminnow consumed more large-bodied prey, such as fish and earthworms, relative to reference-reach fish. In contrast, we detected few differences in prickly sculpin diets between reaches, and the restored reach contained higher densities of smaller sculpin. Thus, the restored reach may be incapable of supporting high densities of large-bodied sculpin.

The observed variation in the diet and population attributes of the fishes we sampled likely reflects differences in macroinvertebrate community structure, habitat, or both factors between reaches. Macroinvertebrate biomass is significantly lower in the restored reach (Albertson et al. 2011), which may have induced restored-reach pikeminnow to adopt a feeding strategy that targeted large-bodied prey such as fish, worms, and gastropods rather than aquatic insects. Pikeminnow tend to principally depend on macroinvertebrates as juveniles and shift diet towards larger prey with increasing age (Moyle 2002, Nobriga et al. 2006). Furthermore, flow preference varies with size: small juvenile pikeminnow require slack water for habitat and larger-bodied individuals tend to select higher velocity flows to feed (Harvey and Nakamoto 1999, Harvey et al. 2002, Gard 2005). Therefore, elevated current velocities — a relative paucity of flow refuges associated with complex habitat such as large woody debris and reduced macroinvertebrate abundance — likely render the restored reach more suitable for large-bodied pikeminnow and limit the density of juveniles. Prickly sculpin were obligate caddisfly (especially *Hydropsyche*) predators during the period we sampled, and *Hydropsyche* densities (by count) in the restored reach are approximately only 36% of levels observed in the reference reach, perhaps due to high substrate mobility (Albertson et al. 2011). However, the relative lack of fine sediments in the restored reach likely rendered habitat in the restored reach more favorable for sculpin by providing access to prey (Harvey et al. 2009) and refuge from predators (Harvey et al. 2004).

Stable isotope patterns suggest that the principal primary production source supporting key macroinvertebrate consumers differs between the restored and reference reaches, with potential consequences for all resident fish species that depend on these organisms for prey. Dominant carbon sources for two macroinvertebrate consumers we assessed shifted from a mix of filamentous algae and FTOM in the reference section to benthic algae (most likely diatoms) in the restored reach. However, a caveat is that the relative contribution of filamentous algae to one assessed consumer (*Hydropsyche*) was highly uncertain, potentially because this taxon is an opportunistic omnivore with considerable dietary heterogeneity (Fuller and Mackay 1981). Numerous Central Valley freshwater fish species, aside from the two we considered (and including Chinook salmon), depend on macroinvertebrates as prey, suggesting that the restoration project could represent a change in primary carbon sources for a significant proportion of the ichthyofauna. The difference in carbon signatures between reaches observed in macroinvertebrates implies that restoration of salmonid spawning habitat could induce impacts to localized populations of omnivorous fishes by locally altering dominant primary production sources.

Although the evidence presented here suggests differences in non-target fish population attributes between an engineered and control reach, we recognize that our results must be viewed in the context of the study scope. The most significant limitation of this study is the short time scale, which likely caused us to overlook variability in fish metrics (especially diet composition) and food web dynamics associated with seasonal changes. Diet composition of most lotic fishes typically varies among seasons (Nakamoto and Harvey 2003), although prickly sculpin diets are often temporally homogeneous (Broadway and Moyle 1978, Tabor et al. 2007). Furthermore, isotopic signatures in streams are often temporally dynamic, especially when flow is highly variable (Finlay et al. 1999, Thompson and Townsend 1999, Zah et al. 2001). Our data were collected in late summer, approximately two months after base flows had been maintained at a constant level (~6.4 $m^3 s^{-1}$) following a flood pulse applied to assist emigration of salmon smolts. We deliberately chose summer, which is the warmest (and, thus, most metabolically demanding due to elevated temperatures) season of the year when climatic conditions are largely homogeneous and access to the river was most reliable. Therefore, although our results report findings representative of a critical period, discerning habitat suitability for non-game fishes in the MRSHEP reach during other seasons will require additional efforts. Our analyses assumed that fish acquired their prey in the location where they were captured. Fish are highly mobile organisms, and although the size of the two study reaches gives us some level of confidence in this assumption, we recognize that fish may acquire resources outside the area where they are captured, particularly large-bodied pikeminnow (Harvey and Nakamoto 1999).

Despite such potential limitations, our results suggest restored salmonid habitat can represent fundamentally different conditions for non-target fish species in stream ecosystems. Multiple population and diet attributes of two non-target fish species in the MRSHEP reach differed significantly from locations upstream. A proportion of such variability may be attributed to differences in food web structure, which was found to differ significantly between reaches. Assessments of lotic food web structure have been particularly lacking in post-restoration project monitoring (Lake et al. 2007), and results presented herein suggest that habitat manipulation alone may shift the dominant carbon source that consumers such as fish depend on. Efforts to restore lotic systems are likely to increase in the future as native fish populations and ecosystem services of rivers continue to decline. Our analyses, along with a growing number of post-manipulation assessments of project efficacy (Palmer et al. 2005, Simon et al. 2007, Korsu et al. 2010), demonstrate the potential for unforeseen responses to ensue in restored systems.

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