Juvenile Chinook salmon, *Oncorhynchus tshawytscha,* growth and diet in riverine habitat engineered to improve conditions for spawning

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Abstract   Many habitat enhancement techniques aimed at restoring salmonid populations have not been comprehensively assessed. The growth and diet of juvenile Chinook salmon, *Oncorhynchus tshawytscha* (Walbaum), rearing in a reach designed to enhance spawning were evaluated to determine how a non-target life stage fared in the engineered habitat. Prior work demonstrated differences in food web structure between restored and unenhanced reaches of the Merced River, thus juvenile salmon feeding dynamics were also hypothesised to vary. Dependent variables were compared among fish collected from within and near the upper boundary of the restored reach and in an unenhanced habitat upstream. Diets, otolith-derived growth and stable isotope-inferred trophic positions were compared. Baetidae mayflies were particularly important prey in the restored reach, while elsewhere individuals exhibited heterogeneous diets. Salmon residing at the bottom of the restored reach exhibited slightly faster growth rates relative to fish collected elsewhere, although stable isotope and diet analyses suggested that they fed at a relatively low trophic position. Specialised *Baetis* predation and/or abundant interstitial refugia potentially improved rearing conditions in the restored reach. Data suggest that gravel enhancement and channel realignment designed to augment adult spawning habitat may simultaneously support juvenile Chinook salmon despite low invertebrate food resources.

KEYWORDS: habitat restoration, Chinook salmon (*Oncorhynchus tshawytscha*), Merced River, food web, growth.

Introduction

Restoring anadromous salmonid populations through habitat enhancement is inherently difficult because of the complex life history attributes of these species (Williams *et al.* 1999; Roni *et al.* 2002; Lackey 2003). One reason why enhancement projects are difficult is that target conditions for one river-dependent life stage may inadvertently affect another life stage. For example, a decline in suitable spawning habitat is often hypothesised to be one of the key bottlenecks that limit the recovery of salmonid populations in degraded

aquatic habitats (Ruckelshaus *et al.* 2002; Honea *et al.* 2009). As such, salmonid restoration efforts frequently aim to increase adult spawning habitat availability. One technique used to enhance spawning habitat is gravel augmentation, in which sediments of a size considered suitable for spawning are added in bulk to stream channels. But what is seldom considered in gravel augmentation projects is that the altered size, heterogeneity and increased mobility of unsorted bed materials could alter the food web in ways that might influence other life history stages of the focal species. To assess the net impact of enhancement techniques, it

is imperative that the direct as well as indirect impacts of enhancement projects on all life history stages are considered.

Widespread reduction of Chinook salmon, *Oncorhynchus tshawytscha* (Walbaum), abundance in California has prompted multiple stream habitat manipulation projects meant to restore populations (Williams 2006; Kondolf *et al.* 2008), many of which target a single or limited number of life stages. Spawning habitat degradation in natal rivers induced by hydraulic mining, dams and water diversion is believed to be a principle impediment to salmon recovery (Yoshiyama *et al.* 1998, 2000; Zeug *et al.* 2011). Consequently, many agencies tasked with restoring populations have attempted to enhance spawning potential by reconfiguring entire channels and/or depositing sediments considered favourable for reproductive adults and incubating eggs (Kondolf *et al.* 1996; Kondolf 2000; Merz *et al.* 2008). The quality of such engineered habitat for juveniles rearing in their natal rivers remains largely unknown, yet elucidating the effects of large-scale spawning habitat remediation on juvenile salmon rearing conditions is necessary to gauge the value of such management actions holistically, as parr growth rates may influence survival during later life stages (Quinn & Peterson 1996; Moss *et al.* 2005).

A number of factors likely cause rearing and feeding conditions for juvenile salmon to vary between channels engineered to promote spawning and unenhanced habitat. Macroinvertebrate prey abundance has been shown to differ in reaches augmented with gravel: post-restoration project surveys have noted elevated (Merz & Chan 2005), depressed (Albertson *et al.* 2011) and equivalent (Sarriquet *et al.* 2007) densities of benthic macroinvertebrates in restored relative to adjacent reaches. Channels augmented with coarse gravel lacking fines may promote prey capture success and prevent antagonistic interactions between individual fish by providing abundant interstitial space as habitat (Suttle *et al.* 2004; Harvey *et al.* 2009). Finally, channel realignment may remove riparian zone vegetation during the construction phase, potentially affecting the abundance of terrestrial insects that are often important prey for salmonids (Wipfli 1997; Utz & Hartman 2007; Rundio & Lindley 2008). Unfortunately, studies that have directly quantified juvenile salmon feeding or growth metrics in habitat enhanced to promote spawning are lacking.

Here, the diets and growth rates of juvenile salmon from within and upstream of a 2.7-km-long section of the Merced River that was engineered to promote adult passage and spawning are compared. Because fish collected within the restored reach were concentrated near the upper and lower boundaries of the restored channel, rearing conditions among three locations were assessed: near the downstream and upstream boundaries of the restored reach (hereafter the restored-bottom and restored-top reaches) and in unenhanced habitat immediately upstream (hereafter the control reach). The following questions were posited. Do parr residing near the upper or lower boundaries of the restored reach of the Merced River: (1) capture a disparate amount of prey; (2) derive energy from different sources; and/or (3) exhibit faster or slower growth relative to fish inhabiting the control reach? To meet study objectives, the diet, trophic position (using $\delta^{13}C$ and $\delta^{15}N$ signatures relative to the food web) and otolith-derived growth rates of wild-origin Merced River juvenile Chinook salmon were quantified in each of the three locations of interest. The study approach included complementary data representative of multiple timescales (e.g. otolith records depicting cumulative growth to diet analyses). Findings from this study may therefore provide a reasonable assessment of how juvenile salmon fare in similarly implemented restoration projects elsewhere.

Methods

Study site

The Merced River is a tributary of the San Joaquin River that drains 33 000 km^2 in the Central Valley and Sierra Nevada region of central California (Fig. 1) and represents the southern-most extent of the current native Chinook salmon range. Salmon is confined to a 39 km reach below the Crocker-Hoffman Dam that blocks upstream fish passage. As in most Central Valley rivers, spawning habitat in the Merced has been severely degraded by gravel mining and the loss of sediment delivery induced by impoundments. Consequently, salmon abundance is critically low: the spring-run has been extirpated and the current hatchery-supported autumn-run population likely represents a fraction of the historic size (Yoshiyama *et al.* 1998; California Department of Fish and Game 2011).

The largest effort implemented to restore salmon populations in the Merced was the Merced River Salmon Habitat Enhancement project (MRSHEP). The project involved a 2.7 km reach where levee failure during a 1997 spring flood event redirected flow to formerly mined land. As a result, pre-restoration conditions in the MRSHEP reach consisted of shallow, slow-moving and occasionally ponded habitat. Although pre-restoration biological surveys were not
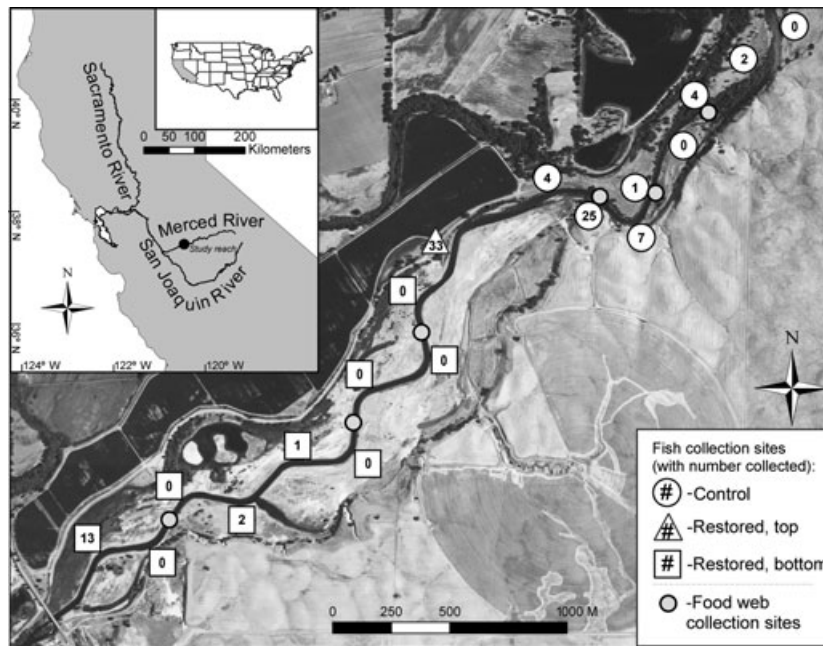
Figure 1. Map and satellite imagery of the Merced River Salmon Habitat Enhancement Project and study sites upstream. Sampling locations, including the number of fish collected, are provided.

conducted, agencies charged with restoration considered the habitat in this reach unsuitable for salmon migration because of the risk of adult stranding and likelihood that such habitat would support high densities of introduced predators of juveniles such as largemouth bass, *Micropterus salmoides* (Lesueur) (California Department of Water Resources 2001, United States Fish and Wildlife Service 2001). In attempt to improve conditions for salmon migration, spawning and rearing in this reach, the California Bay-Delta Authority (CALFED) implemented a large-scale habitat restoration project that was completed in 2001. The MRSHEP reach and adjacent floodplain were re-graded with heavy machinery to create a single channel with a meandering plan form and riffle-pool sequences (California Department of Water Resources 2001; Fig. 1). Following channel realignment, about 1.5 million tonnes of coarse sediment were added to the reconfigured section. The restored reach was specifically designed to allow processes such as point bar evolution, pool and riffle formation, and sediment transport to ensue naturally under the current dam-controlled flow regime. Although channel evolution has been minor since project completion, a small degree of natural point bar evolution has occurred near the upstream end of the reach (Legleiter *et al.* 2011). Procedures applied in the MRSHEP (such as gravel augmentation and channel realignment) are very common in degraded Central

Valley rivers of California (Kondolf 1998; Merz & Setka 2004; Marshall *et al.* 2008).

Study design

An ideal situation for assessing the impact of a restoration or enhancement effort is to have a BACI (before/after, control/impact) study design (Kondolf 1995; Miller *et al.* 2010). Unfortunately, like many river restoration projects (Kondolf *et al.* 2007; Rumps *et al.* 2007; Reiser 2008), no funding was allocated for pre-project monitoring. In the absence of any historical data, options for gaining inference about the impacts of restoration have been spatial comparisons to other rivers, or in this case, spatial comparisons between engineered habitat and locations unaffected by the 1997 events that initiated restoration. Thus, the possibility exists that differences in biological attributes detected between control habitat and the MRSHEP reach pre-date restoration efforts. However, this is unlikely because the MRSHEP construction procedure involved complete realignment of the channel and floodplain, resulting in a post-restoration reach that was substantially narrower, deeper and with an entirely novel sediment regime relative to the slough-like pre-restoration conditions.

Study sites were located within the MRSHEP reach as well as directly (≥1.7 km) upstream (referred to as

the restored and control reaches, respectively). Although collection efforts initially targeted salmon from the entire study area, the majority of restored-reach fish were found in either the uppermost or bottommost pool-riffle sequence, with only two fish collected in between. Therefore, to evaluate conditions for juvenile salmon in the restored reach, comparisons were made among the diet and growth attributes of fish collected from the control reach, near the upstream end of the restored reach, and in the downstream end of the restored reach (to determine whether there were spatial patterns in feeding and growth conditions within the restored reach).

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 control reach is wider and shallower than the restored reach. Deep, high-flow velocity pools are the dominant habitat unit in the restored reach, while shallow runs dominate the control reach. Because the restored reach channel is approximately 20% narrower but conveys the same discharge, average flow velocity is greater. Large woody debris is more abundant and consists of larger pieces (by volume) in the control reach. The riparian zone throughout the study area is likely less extensive in comparison with conditions prior to agricultural expansion in the Central Valley (Hunter *et al.* 1999). Deciduous trees are present in the control 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 lower in the restored reach. However, the lack of riparian cover apparently does not increase radiant warming much, perhaps because of adequate hyporheic exchange in the restored reach. The difference in mean daily temperature during September and October (both months are typically warm with low cloud-cover in the region) 2008 between the uppermost and lowermost sampling location was 0.2 °C. Although the median particle size is similar between reaches, this reflects a similarity along a single point in the distribution: fine sediments concentrations are substantially lower in the restored reach (Table 1; California Department of Water Resources 2006). Sediments are more embedded and compacted in the control reach, largely as a result of elevated concentrations of fine sediment (Albertson *et al.* 2011). A minority of attributes, such as channel depth and slope, are similar throughout the study area.

Differences in biological attributes have also been detected between the restored and control reaches. Total macroinvertebrate abundance and biomass were typically lower in the restored reach, and the benthic macroinvertebrate community was numerically dominated by filter-feeding, sedentary *Hydropsyche* in the control reach compared with collector/grazer, and more mobile species (e.g. *Baetis*) in the restored reach (Albertson *et al.* 2011). Experiments performed by

Table 1. Physical habitat attributes compared between the restored and control reaches of the Merced River

Variable	Method[data source]	Control	Restored
Slope ($\times 10^{-3}$)	Comprehensive survey of both reaches[†]	2.6	2.5
Proportion of pool:riffle:run (by area)	Comprehensive survey of both reaches[†]	0.15/0.31/0.54	0.39/0.24/0.37
Bankfull width (m)	Mean from 1 m interval transects[†]	35.3	29.2
Wetted width (m)*	Mean from 1 m interval transects[†]	24.9	19.8
Mean depth (m)*	Mean from 1×1 m grid[†]	0.6	0.5
Mean velocity (m s^{-1})*	Mean from 1×1 m grid[†]	0.4	0.6
Embeddedness (%)	Following Bain (1999), two grids assessed per reach[‡]	6.3	0.5
Compactedness (N)	Following Downes *et al.* (1997), two measurements per reach[‡]	24.0	20.3
Median particle size (cm)	Two 100-sample pebble counts per reach[‡]	6.4	5.7
Fine sediment concentration (%)	Number 0.5 m^2 quadrat intersections on fines-6 random samples per reach	6.3	0.5
Undercut banks (% of surveyed length)	Measured along 1500-m section per reach[‡]	4.7	0.0
Wood density (*n* pieces per 100 m^{-2})	Measured within wetted channel of 1 500-m section per reach[‡]	5.0	0.2
Mean wood volume ($\times 10^{-2}$ m^{-3})	Derived from length and width of all pieces in 500-m section per reach[‡]	1.5	0.7
Shade cover (%)	Standard spherical densiometer readings every 25 m in 500-m sections, taken 1 m from bank[‡]	32.0	0.2

*Values at standard baseflow (6.4 m^3 s^{-1}; California Department of Water Resources 2011).

Data were derived from [†]Harrison *et al.* (2011) or [‡]Albertson *et al.* (in press) as noted.

Albertson *et al.* (2011) suggested that these differences are because of increased bed mobility and/or increased homogeneity of bed particles in the restored reach. The impacts of the project on the local salmon population remain unknown (Marshall *et al.* 2008).

Field and laboratory procedures

Sampling effort was planned to collect 50 juvenile Chinook salmon from throughout each of the restored and control reaches. Ten pool-riffle sequences within the restored reach and eight in the reference reach spaced approximately 280 m apart were sampled by seining approximately 40 m of habitat (Fig. 1). The uppermost sampling location was approximately 11 river kilometres downstream of the Crocker-Hoffman dam, where adult salmon are prohibited from migrating further upstream. Collections were conducted between 3 and 5 April 2009 during the morning (07:00–11:00). Juvenile salmon were euthanised on-site and stored frozen. Although a hatchery operates just below the Crocker-Hoffman dam upstream of the study site, all hatchery-produced salmon in 2009 were released at Jersey Point in the Sacramento-San Joaquin Delta (∼175 river km downstream of the study area), and escape prior to release was considered extremely unlikely (M. Cozart, California Department of Fish and Game, personal communication). All collected fish were therefore assumed to be of wild origin.

Additional data were collected to complement analyses of fish feeding and growth. Samples of primary producers and macroinvertebrates were collected to quantify the Merced River food web using $\delta^{13}C$ and $\delta^{15}N$ values. Three replicates of each food web component were sampled from six sites within the control and restored reaches (see Fig. 1 for locations). Riparian tree leaves and grasses were collected by hand, and benthic algae were sampled by scraping material off large rocks using a knife blade. Stream water was sieved to amass samples of fine transported organic matter (FTOM) consisting of particles < 1000 and > 100 μm. Macroinvertebrates, filamentous algae and aquatic macrophytes were sorted from material collected using a 1-m wide, 500-μm-mesh kick-net. Drifting invertebrates were passively sampled using 47×28 cm frame, 500-μm-mesh drift nets over approximately 24-h periods on 4 and 9 April 2009 at the food web sampling locations (Fig. 1). All samples were placed in plastic bags and stored frozen. Temperature loggers that recorded data at 20-min intervals were deployed throughout the study reach to identify any thermal regime differences between sections.

Fish were thawed and processed in the laboratory. Fork length to the nearest mm and weight to 0.1 g were recorded prior to dissection. Stomach contents were extracted, distinguishable items were identified to genus or the lowest taxonomic level possible under a dissecting microscope, and all contents were then dried to determine total consumed mass per stomach. Mean dry mass for each prey taxon was derived by randomly selecting 25–200 (depending on rarity) individuals from the drift- or kick-net collections that were dried and weighed to provide estimates that accounted for differential rates of digestion (Hyslop 1980; Eberle & Stanford 2010). The dry mass of each prey type per stomach was estimated by multiplying the mean dry weight of the undigested prey item (derived from the drift or kick subsamples) by the number of organisms observed. Pure white muscle tissue samples were extracted from each fish, rinsed with deionised water, dried at 60 °C for 48 h and ground with a mortar and pestle in preparation for isotopic analysis.

Salmon sagittal otoliths were removed from the carcass, rinsed first with bleach and then deionised water, air dried, and stored as outlined by Secor *et al.* (1991). Otolith analytical procedures followed Zhang *et al.* (1995). The sagittal plane of the left otolith was polished except for in cases where it was accidently damaged during the process, in which case the right otolith was polished. The widths of all discernable daily growth measurements were measured along a line from the primordia to the dorsal end that was perpendicular to the anterior–posterior axis. Rings that represented the transition from egg to alevin and the onset of exogenous feeding (hereafter the hatch and first-feeding checks) were identified to determine which increments reflected growth derived from external feeding.

Samples of primary producers and macroinvertebrates were prepared for $\delta^{13}C$ and $\delta^{15}N$ analysis. Samples of terrestrial leaves, aquatic macrophytes and filamentous algae were rinsed with deionised water, dried at 60 °C for 48 h and ground with a mortar and pestle. Select macroinvertebrate taxa that were common in the diet and/or abundant in the benthic kick-net samples were identified, rinsed, oven-dried, ground and acidified with 10% HCl to remove inorganic carbonates in the exoskeleton. Benthic algae and FTOM samples were purified of inorganic materials using centrifugation in colloidal silica as outlined by Hamilton *et al.* (2005), collected on glass fibre filters and oven-dried. Subsamples of all dried and ground or filtered organic materials were pressed into tin capsules and sent to the Marine Science Institute Analytical

Laboratory at the University of California, Santa Barbara, for isotopic analysis.

Statistical analyses

Comparisons were made among three groups based on collection location: fish collected at the downstream end of the restored reach, those collected at the top of the restored reach (the restored-bottom and restored-top reaches, respectively), and those collected in the control reach (see Fig. 1 for the locations of each classification). The three-tiered designation was applied to determine whether fish exhibited differences in diet and growth metrics within the restored reach as well as compared with the control reach.

Diet data were assessed using a mix of univariate and multivariate approaches. After checking for homogeneity of variances among reaches using Levene's test (Levene 1960), measured organic matter mass and estimated total dry mass were compared using an analysis of variance (ANOVA) and subsequent post hoc Tukey HSD comparisons. Overall differences in prey composition by relativised weight among reaches were detected using analysis of similarity (ANOSIM; Clark 1993), and prey type-specific differences were identified via indicator species analysis (McCune & Grace 2002). Additionally, the dietary niche width and degree of specialisation among treatments were assessed by plotting the frequency of occurrence for each prey against the corresponding specific abundance (proportion of the total diet by mass a prey class represents when present in the stomach) as outlined by Amundsen et al. (1996).

Growth rates were estimated following the methodology of Titus et al. (2004). Fish size at the onset of feeding was back-calculated using the Fraser-Lee method:

$$FL_f = [O_f \times (FL_c - a)/O_c] - a$$

where FL_f is fish length at first feeding, FL_c fish length at capture, O_f the otolith width at first feeding, O_c the otolith width at capture, and a the intercept of the regression of fish length on otolith width. To calculate growth rates, gain in length between first feeding and capture was divided by the number of rings present after the onset of feeding. The condition factor of fish among the three reaches was also compared following Anderson et al. (1996):

$$\text{Condition factor} = 10\,000 \times \text{Weight (g)} / \text{Length}^3 (\text{mm})$$

After checking for homogeneity of variances in growth rates and condition factor among reaches using Levene's test, values were compared in an ANOVA model and subsequent post hoc Tukey HSD comparisons.

δC^{13} and δN^{15} were initially collected to quantify the relative contribution of allochthonous and autochthonous primary production sources to salmon tissue (i.e. Moore & Semmens 2008). However, preliminary analyses revealed that fish had not grown enough to allow δC^{13} to come into equilibrium with their diet, as salmon tissue signatures exceeded those of all other food web components and declined with fish size (Fig. 2). Such trends indicate that tissue signatures were still influenced by marine-derived nutrients derived from yolk metabolism (Perry et al. 2003). Furthermore, preliminary analyses suggested that δC^{13} signatures of many lotic food web components, including juvenile salmon, exhibited a consistent spatial gradient based on collection location. Because δN^{15} in salmon tissue had apparently stabilised for fish
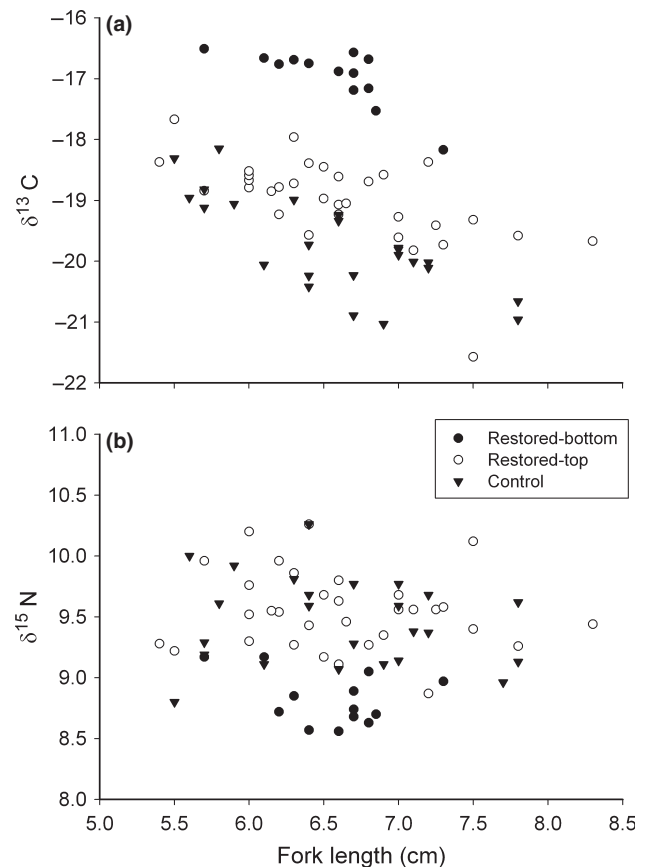
Figure 2. Juvenile salmon white muscle tissue (a) δC^{13} and (b) δN^{15} variation as a function of fish size delineated by reach.

$\geq$5 cm (Fig. 2) and δN^{15} signatures of most food web components exhibited no consistent spatial trend, the trophic position (Cabana & Rasmussen 1996) of juvenile salmon was compared among the three reaches using:

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

where *TP* is trophic position, the N^{15} of primary consumers is the pooled mean value among *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 salmon stomachs and the taxon is numerically dominant in the macroinvertebrate community, particularly in the restored reach (Albertson *et al.* 2011).

Results

Although juvenile salmon were found at all sampling stations throughout the control reach (*n* = 43), nearly all salmon collected in the restored reach were found either at the uppermost (*n* = 33) or lowermost (*n* = 13) sampling locations (Fig. 1). Salmon were present in 60.0% of the sampled pool-riffle sequences in the control reach but only 26.7% of sites in the restored reach. Fish size varied among sites: nearly one-third of salmon collected in the control reach was < 5 cm long, while only three individuals (6%) in the restored reach were within this size range (Fig. 3). Comparisons of diet, growth and stable isotope attributes of salmon were restricted to fish $\geq$5 cm long because small fish possess gapes that preclude them from feeding on certain prey and the lack of < 5 cm collected salmon within the restored reach.

Significant differences in stomach content mass and diet composition were observed among reaches. Both

Figure 3. Length-frequency histogram of juvenile salmon collected in the Merced River delineated by treatment reaches.

estimated ($F_{2,68} = 5.1$, $P = 0.0085$) and measured ($F_{2,68} = 13.5$, $P < 0.0001$) consumed prey dry mass significantly differed between reaches (Table 2). Fish feeding in the bottom of the restored reach consumed the least by both measures. However, when quantifying prey mass directly, the restored-top reach content mass ranked highest, while estimated content mass was highest in the control reach. Five invertebrates (amphipods, *Baetis* larvae, Chironomidae larvae, *Hydropsyche* larvae and isopods) contributed > 85% of all estimated prey by mass. Each prey item was categorised into these and five additional groups to test for differences of specific prey consumption among reaches. An ANOSIM model suggested that significant overall compositional differences in relativised mass data among reaches ($R = 0.2933$, $P = 0.0001$) were evident. Subsequent indicator species analysis identified several significant prey categories in each reach (Table 3): control-reach diets were characterised by *Hydropsyche* larvae, chironomid larvae, and *Acarina* (water mites), fish in the top of the restored reach consumed significantly more isopods and non-*Baetis* mayflies (mostly *Serratella*), while diets in the bottom of the restored reach were significantly dominated by *Baetis*. Amundsen prey frequency-abundance biplots (Fig. 4) suggested that salmon in the bottom of the restored reach are *Baetis* specialists, while those in the top of the restored reach and the control reach are more generalist feeders although *Hydropsyche* larvae appear to be particularly important prey for control-reach salmon.

Mean *Baetis* count per fish was compared among reaches because *Baetis* appeared to be a critical prey taxon, particularly for restored-bottom salmon. Square-root transformed mean *Baetis* counts were significantly higher in restored-bottom fish relative to the other two reaches ($F_{2,68} = 33.5$, $P < 0.0001$; Table 2).

Growth rates significantly varied among reaches ($F_{2,68} = 3.9$, $P = 0.0278$; Table 2). *Post hoc* comparisons suggested that salmon in the restored-bottom reach grew slightly, but significantly, faster than those in the restored-top reach, while growth rates in the control reach were not significantly different from those observed in either of the other reaches. Differences in growth rates were unlikely caused by variation in temperature: the mean daily water temperature between 15 February and 3 April (approximately the range of dates that represent external feeding for $\geq$5 cm salmon in this study) at the uppermost control reach collection location was 12.56 °C compared with 12.65 °C in the downstream end of the restored reach. No significant differences in condition factor among
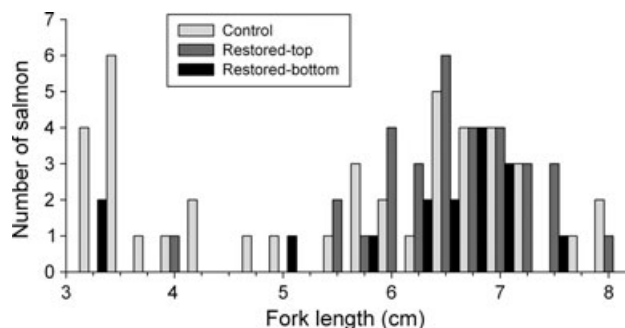
Table 2. Attributes of juvenile Chinook salmon among study reaches. Data represent only fish ≥5 cm long. Shown are means ± 1 standard error. Superscripted letters denote significant differences determined using Tukey's HSD comparisons

	Treatment reach		
Variable	Control	Restored-top	Restored-bottom
Measured stomach content mass (mg)	19.2 ± 2.3^A	25.1 ± 1.9^A	9.6 ± 1.8^B
Estimated stomach content mass (mg)	41.5 ± 7.0^A	29.8 ± 6.6^{AB}	20.4 ± 3.8^B
Baetis count	2.8 ± 0.5^A	1.2 ± 0.2^A	8.2 ± 1.0^B
Growth rate (mm day^{-1})	$0.75 \pm .03^{AB}$	0.73 ± 0.03^B	0.84 ± 0.02^A
Condition factor	1.20 ± 0.02	1.22 ± 0.02	1.24 ± 0.04
Trophic position	3.45 ± 0.02^A	3.48 ± 0.02^A	3.27 ± 0.02^B

Table 3. Indicator species analysis parameters for prey consumed by juvenile Chinook salmon among study reaches. Mass values were relativised by prey category prior to analysis. Bold values indicate statistically significant indicator prey

Prey	Reach with highest value	Indicator value	*P*-value
Acarina	Control	**86.6**	**0.0002**
Amphipods	Restored-top	17.8	0.0696
Baetis	Restored-bottom	**67.5**	**0.0002**
Chironomids	Control	**65.5**	**0.0002**
Hydropsyche	Control	**34.9**	**0.0130**
Isopods	Restored-top	**36.5**	**0.0086**
Other aquatic insects	Control	12.6	0.1808
Other mayflies	Restored-top	**41.7**	**0.0194**
Other caddisflies	Control	15.4	0.0986
Terrestrial arthropods	Control	32.6	0.0914

reaches were detected ($F_{2,68} = 0.5$, $P = 0.6045$; Table 2).

Salmon tissue δC^{13} values decline as a function of fish size (Fig. 2a), strongly suggesting that signatures partly reflected the metabolism of marine-derived yolk. However, δN^{15} signatures appeared to have stabilised by the time fish were collected (Fig. 4b). Salmon trophic position significantly varied among reaches ($F_{2,68} = 24.4$, $P < 0.0001$). Statistically significant differences in trophic position were limited to fish in the restored-bottom reach, where values were lowest, compared with those observed in the other two reaches (Table 2). Such variability in trophic position among reaches corresponded with the observed differences in diet composition, as *Baetis* possessed the lowest δN^{15} values (4.5 ± 0.2; mean ± 95% confidence intervals) relative to all other assessed invertebrates (5.0 ± 0.2, 5.8 ± 0.2, 6.0 ± 0.1, 6.2 ± 0.3 for *Hydropsyche*, Elmid beetle larvae, isopods, and *Isoperla* stoneflies, respectively) except Chironomidae (4.1 ± 0.2).

Discussion

Findings suggest that a channel engineered to enhance adult Chinook salmon spawning and migration offers suitable, and possibly moderately more favourable, feeding and rearing conditions for juveniles relative to unenhanced riverine habitat. Salmon collected near the lower boundary of the restored reach were feeding at a lower trophic level yet exhibit equivalent or slightly faster growth rates and consumed significantly more *Baetis* mayflies relative to locations elsewhere. Feeding conditions near the upstream boundary of the restored reach appeared to resemble more closely those in the control reach, as diet, δN^{15} signatures and growth rates in these two sections were more similar to each other relative to fish collected in the restored-bottom reach. The similarity in feeding and growth attributes between the restored-top and control reaches may reflect patterns in drift composition, as drifting prey like *Baetis* in the restored-top reach was likely derived from upstream of the restoration boundary. Although differences were minor, statistically significant variations in salmon growth were only evident between fish of the restored-top and restored-bottom reaches. Thus, results suggest that individuals rearing near the lower boundary of the restored channel were at least as capable of achieving equivalent growth compared with fish upstream of the restoration boundary and able to grow more rapidly than fish in the restored-top reach. These results help to fill a critical knowledge gap in river restoration aimed at recovering stocks of
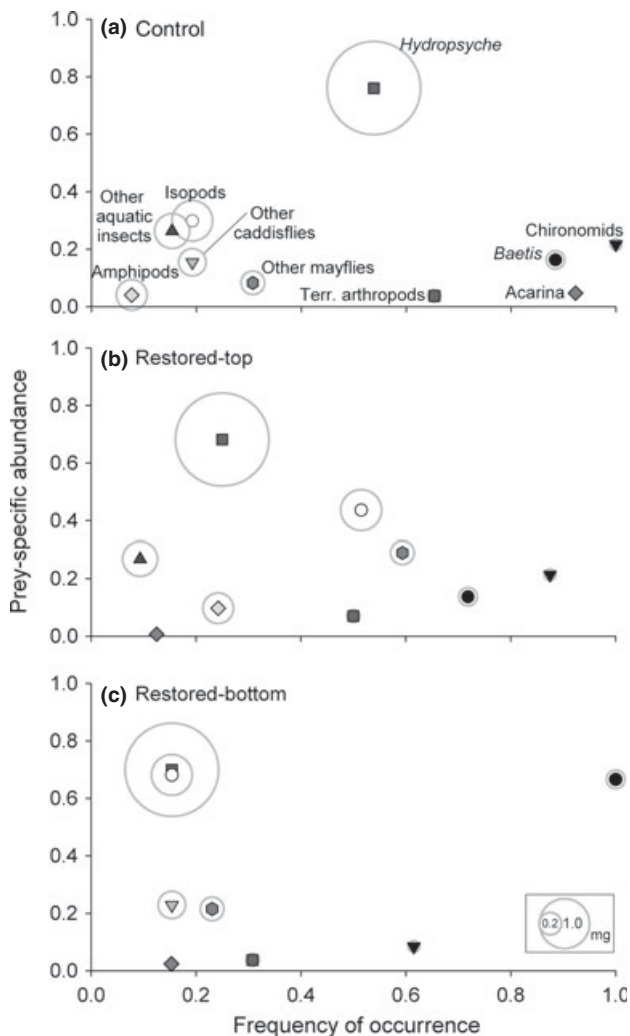
Figure 4. Specific abundance and relative frequency biplots (Amundsen *et al.* 1996) of prey consumed by ≥5-cm-length juvenile Chinook salmon in the (a) control, (b) restored-top and (c) restored-bottom reaches of the Merced River. The *x*-axis represents the frequency in which the prey is encountered, the *y*-axis denotes the mean proportion of the total diet (by mass) each prey contributes when present in a stomach. Circles surrounding each point represent the mean undigested prey dry mass (mg).

anadromous salmonids, as studies that have quantified juvenile salmon growth or diet *in situ* within an engineered channel are lacking.

Variability in the sediment regime among reaches may have contributed to observed growth patterns among sites. High fine sediment concentrations in benthic substrates reduce the availability of macroinvertebrate prey and increase the amount of energy fish expend on swimming and aggression because of interstitial flow refugia loss, consequently reducing the growth rates of juvenile salmonids (Suttle *et al.* 2004; Harvey *et al.* 2009). Concentrations of fines in

the MRSHEP reach are very low in comparison with the relatively embedded control reach, most likely due to the deposition of 1.5 million tonnes of coarse (primarily ≥55 mm) gravel as part of the project. Thus, salmon rearing in the restored reach may have been able to achieve equivalent to slightly faster growth rates relative to fish rearing elsewhere because of favourable benthic habitat despite relatively lower levels of macroinvertebrate biomass in the section (Albertson *et al.* 2011). Unfortunately, the large size of the Merced River and low density of juvenile salmon prevented microhabitat use surveys being conducted to complement diet and growth analyses. Another macroinvertebrate-feeding fish species [juvenile Sacramento pikeminnow, *Ptychocheilus grandis* (Ayres)] has also exhibited elevated growth rates in the MRSHEP reach while consuming a roughly equivalent amount of *Baetis* larvae compared with control-reach individuals (M. Romanov, J. Hardy, S.C. Zeug & B.J. Cardinale, unpublished data). Therefore, the relative abundance of interstitial habitat in the restored reach represents a possible explanation for the observed trends in fish growth rates associated with the MRSHEP.

Alternatively, the observed patterns in growth rates among reaches may have plausibly been caused by differences in diet. Fish near the lower boundary of the MRSHEP reach consumed significantly more *Baetis* larvae relative to those collected upstream, where salmon fed on a heterogeneous mix of very small-bodied prey and the occasional large-bodied *Hydropsyche*. Such variation in diet corresponds with observed differences in macroinvertebrate community structure between reaches: Albertson *et al.* (2011) concluded that *Baetis* and *Hydropsyche* numerically dominate the restored and control-reach macroinvertebrate assemblages, respectively (though, total abundance of nearly all taxa, including *Baetis* and *Hydropsyche*, was lower in the restored reach). Although *Hydropsyche* are larger and thus offer more nutrients per capture, only about half of control-reach fish were found with this prey. *Baetis* larvae possess a relatively higher propensity to drift (Rader 1997; Holomuzki & Biggs 2000; Esteban & Marchetti 2004) and juvenile Chinook may prefer mid-water feeding on drift over benthic foraging in riverine habitat (Johnson 2008). Additionally, salmon in the restored-top and control reaches consumed significantly more very small-bodied invertebrates such as water mites and Chironomid fly larvae. The foraging cost per unit of energy gained for small prey is likely high (Rondorf *et al.* 1990). Restored-top and control-reach salmon possessed the highest stomach content masses among groups of fish. However, this trend could reflect

disparities in gastric evacuation associated with a *Hydropsyche*-rich diet, as large prey items tend to be evacuated at much slower rates (Bromley 1994; Pääkkönen *et al.* 1999; Sveier *et al.* 1999). Thus, fish residing near the lower boundary of the restored reach may have been capable of achieving equivalent to slightly faster growth by primarily consuming medium-sized *Baetis* that are prone to drift dispersal.

Regardless of the mechanisms, juvenile Merced River Chinook salmon appeared capable of growing at rates that matched or exceeded those observed in comparable ecosystems. Growth rates in nearby river main-stems within the Central Valley were substantially lower than those reported in the current study: Sommer *et al.* (2001) recorded mean growth rates of wild fish that ranged from 0.43 to 0.52 mm day^{-1} in the Sacramento River, while caged, hatchery-origin individuals experimentally deployed in the Consumnes River main-stem grew between 0.19 and 0.57 mm day^{-1} (Jeffres *et al.* 2008). Chinook salmon rearing in the Central Valley may exhibit overall lower growth rates relative to other regions. For instance, wild and hatchery-origin juveniles rearing in the Snake River main-stem (Idaho, USA) consistently grow at rates within the range of 1.1–1.3 mm day^{-1} (Connor & Burge 2003; Connor *et al.* 2004). Such values suggest that Merced River salmon grew at a relatively average rate relative to conspecific populations during the study period. However, extending comparisons of salmonid growth rates as a proxy to assess habitat quality among regions must be conducted with a high degree of caution, as growth is simultaneously affected by temperature, food quality and quantity and density-dependent effects (Marine & Cech 2004; Geist *et al.* 2011).

Juvenile salmon were unevenly distributed throughout the restored reach, perhaps because of limitations in available habitat and/or an unequal distribution of redds during the preceding spawning season. The two locations where 93% of juvenile salmon were collected within the MRSHEP reach featured a well-developed point bar at the terminus of a riffle (in the restored-top site) and a > 10-m-long, 0.6-m-thick piece of stable large woody debris (the restored-bottom site). Each of these structures likely provided a flow refuge, whereas elsewhere in the MRSHEP reach flow velocities are near-uniformly high (> 0.50 m s^{-1}) and structural habitat is lacking (Harrison *et al.* 2011; Albertson *et al.* in press). By contrast, large woody debris, point bars, undercut banks and other complex habitat features are more common in the control reach (Albertson *et al.* in press). Juvenile Chinook salmon select habitat with flow velocities < 0.25 m s^{-1}

(Holecek *et al.* 2009, Cromwell & Kennedy 2011), most likely to conserve energetic resources while foraging or drift feeding (Rosenfeld & Taylor 2009). Alternatively, the spatial distribution of redds during the preceding spawning season may have been concentrated in the locations where juveniles were most abundant. The two features that likely provided flow refuge for juveniles, a well-developed point bar and large woody debris, also promote favourable conditions for redds that adults select during spawning (Geist & Dauble 1998, Senter & Pasternack 2011). The above hypotheses explaining the distribution of juveniles in the MRSHEP reach are not mutually exclusive. Future efforts that consider juvenile rearing conditions in engineered habitat of the Merced River and elsewhere should consider redd locations and *in situ* observations of habitat use.

While findings suggest that salmon rearing in engineered habitat possessed a different diet and equivalent growth rates relative to fish collected elsewhere, these findings must be viewed in the context of the study scope. Fish were collected during the morning hours, thus stomach samples presumably reflected the period of elevated feeding associated with dawn. While most studies suggest juvenile Chinook are primarily diurnal predators that feed most successfully at dawn and dusk (Sagar & Glova 1988; Schabetsberger *et al.* 2003; Johnson 2008), some populations feed nocturnally (Bradford & Higgins 2001). The macroinvertebrate drift- and kick-net sampling protocol was developed prior to fish sampling and a consequential lack of data at key sites (such as the restored-top site) prevented calculations of prey selectivity. Diets and growth rates were assumed to reflect the feeding opportunities where fish were collected, yet individuals could have grown and fed beyond where they were found. Even so, this is unlikely. The spatially distinct nature of tissue stable isotope signatures (especially for δC^{13}) suggests that the collected juvenile salmon were sedentary. Salmonid growth is known to be density-dependent in streams (Grant & Imre 2005; Einum *et al.* 2006; Crozier *et al.* 2009). The highest density of salmon encountered (0.11 fish m^{-2}, based on the length of channel sampled and size of the seine net at the site with the most salmon) was very low relative to most populations of lotic salmonids, and density-dependent growth of year-0 age salmonids in densities within this range has been shown to be minor or insignificant (Utz & Hartman 2009).

With the above caveats in mind, results suggest that habitat engineered to enhance adult salmon spawning and migration may still provide suitable conditions for juvenile Chinook salmon. An abundance of *Baetis* drift

and/or interstitial space in engineered habitat potentially led to juvenile salmon growth rates that compare with those observed elsewhere in the Merced River. Further work will be necessary to determine whether shifts in feeding strategy or habitat use allow juvenile salmon to achieve high growth rates in restored habitat. In the light of the rapidly expanding scale and extent of salmonid spawning habitat remediation efforts in California (Kondolf 1998; Kondolf *et al.* 2007, 2008) and elsewhere (Rumps *et al.* 2007; Reiser 2008), the results presented here offer vital information with implications concerning the effects of such actions on juvenile rearing conditions. However, these findings also demonstrate the capacity for juvenile salmon diets to differ substantially between restored and un-restored habitat, highlighting the need to consider the potential effects of spawning habitat enhancement on juvenile salmon when this management action is applied.

Acknowledgments

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