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Stream macrophytes increase invertebrate production and fish habitat utilization in a California stream

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Abstract

Stable flow and thermal regimes, coupled with geologically derived nutrients, are drivers of enhanced productivity in volcanic spring-fed rivers. However, little information exists on biotic mechanisms or species interactions contributing to elevated productivity at higher trophic levels. In a California stream, juvenile steelhead trout were observed to preferentially select macrophyte habitat at a rate three times greater, on average, than five other habitat types. To understand the potential rearing benefits associated with macrophytes, we conducted a manipulative experiment to determine how macrophytes affect invertebrate prey availability and stream water velocity. Macrophytes supported up to nine times greater abundance of invertebrates than adjacent open gravel habitats. They also doubled invertebrate drift rates and reduced water velocity by up to 42-fold. The results show that aquatic macrophytes are an important stream habitat feature that may be bioenergetically more favourable for rearing salmonids than more traditional lotic habitats. We suggest that macrophytes have the potential to enhance growth rates of juvenile salmonids when compared with other habitat types. Habitats that confer growth and size advantages may ultimately improve fitness and contribute to conservation of imperilled salmonids.

KEYWORDS

invertebrate production, macrophytes, positive species interactions, salmonid habitat, spring-fed rivers

1 | INTRODUCTION

Macrophytes are a dominant habitat feature in many lowland, nutrient rich, lotic ecosystems (Kaenel & Uehlinger, 1999). Their physical and biological effects on the stream micro-environment are extensive. Macrophytes enhance stream bed stability, reduce water velocity, and increase water depth (Cotton, Wharton, Bass, Heppell, & Wotton, 2006; Fritz, Gangloff, & Feminella, 2004; Gregg & Rose, 1982; Kaenel & Uehlinger, 1999). They provide habitat complexity by directly increasing available surface area (via plant morphology) for invertebrates and epiphytic algae colonization and by providing refuge from predators (Rozas & Odum, 1988; Taniguchi, Nakano, & Tokeshi, 2003). They are known to retain fine particulate organic matter and detritus, important energy sources in food web dynamics (Elger, Barrat-Segretain, & Willby, 2006; Gregg & Rose, 1982; Harrod,

1964; Sand-Jensen, 1998). The importance of macrophytes in lotic ecosystems is clearly substantial; however, few studies have examined their effect on secondary production and drift of invertebrates and their potential importance for rearing of Pacific salmonids (*Oncorhynchus* spp.).

Macrophytes are particularly extensive in spring-fed rivers in volcanic arc terrains; such rivers can be important for rearing of juvenile salmonid fishes (Lusardi, Bogan, Moyle, & Dahlgren, 2016). Macrophyte abundance in these systems is largely a product of water chemistry, stable flow, constant thermal regimes, open canopy, and low gradient. Although macrophytes are known to be important habitat modifiers and provide spatial heterogeneity in streams for invertebrate and epiphytic algae colonization, their role in food webs and other ecological processes is not well defined (Taniguchi et al., 2003). Abiotic variables such as water temperature and flow

are hypothesized to positively affect growth and production of salmonids in volcanic spring-fed rivers (NRC, 2004), but little is known about biotic interactions and the role of macrophytes. Here, we address this knowledge gap and seek to answer the following question: What are the ecological mechanisms associated with macrophyte habitat that benefit higher order consumers, especially juvenile salmonids, in volcanic spring-fed rivers?

Several studies have observed the use of macrophyte habitat by salmonid species, but the potential benefits associated with the use of such habitat have remained elusive. For instance, Chapman (1966) observed the use of macrophyte habitat by juvenile steelhead, and Riley, Pawson, Quayle, and Ives (2009) found that salmonids were more abundant and exhibited higher growth rates where they co-occurred with macrophyte habitat. Defining specific habitat-related mechanisms that influence growth and production of juvenile salmonids is of fundamental importance to their long-term survival. Habitats that confer growth and size advantages may ultimately improve fitness (Bond, Hayes, Hanson, & MacFarlane, 2008) and contribute to the conservation of imperilled salmonids (Moyle, Lusardi, Samuel, & Katz, 2017).

We conducted snorkel surveys to determine salmonid habitat preference and utilization in a volcanic spring-fed river. Based on those results, we then conducted two field experiments at different spatial scales to understand differences in secondary production (prey availability), drift of invertebrates, and hydraulic character at salmonid drift feeding sites. We hypothesized that macrophyte habitat (a) positively affects invertebrate density and drift and (b) negatively affects

water velocity, when compared with adjacent gravel-bed habitat. Our general purpose was to understand the mechanisms contributing to salmonid habitat selection in spring-fed rivers. Our results also provide insight on biotic interactions and their ability to influence productivity at higher trophic levels in stream ecosystems.

2 | METHODS

2.1 | Study area

This study was conducted on the Shasta River in northern California (Figure 1), which drains a semi-arid watershed of approximately 1,900 km². The majority of precipitation in the watershed originates as snow in the higher elevations of the southern Cascades, but the hydrology is impaired at river kilometre (rkm) 65 by Dwinell Dam. Below the dam, the Shasta River is joined by numerous springs, including Big Springs Creek, at rkm 54. Inflow from Big Springs Creek modifies the Shasta River's hydrology by providing groundwater baseflow throughout the year. Salmonid returns on the Shasta River have been drastically reduced compared with historical numbers due in large part to a lack of access to spawning habitat and elevated water temperature associated with agricultural practices on adjacent lands (NRC, 2004). Recent restoration activities, however, have ameliorated some factors limiting salmonid production, prompting this study.

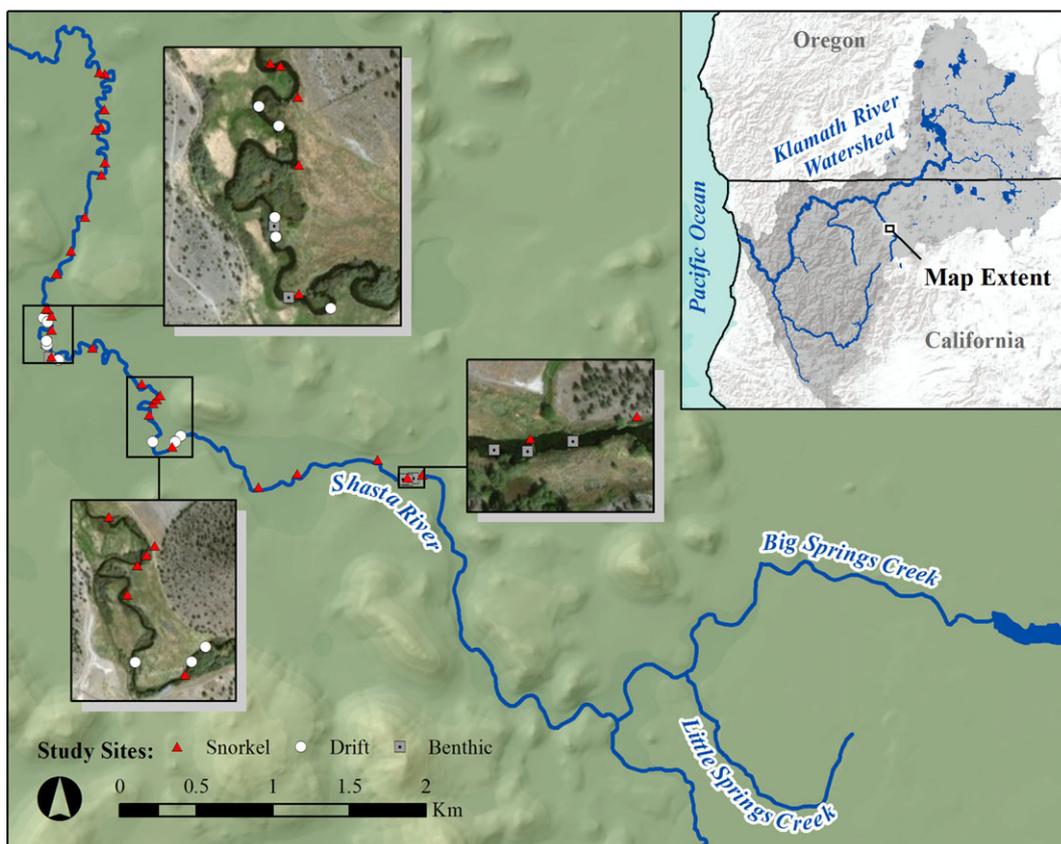


FIGURE 1 Research site on the Shasta River in Siskiyou county, northern California, USA. Research was conducted at the Nelson Ranch property of the Nature Conservancy [Colour figure can be viewed at wileyonlinelibrary.com]

2.2 | Manipulative study experimental design

At the patch scale, five paired replicate plots were established in the Shasta River between rkm 44 and 51.7. Each paired site was selected based on canopy cover, water depth, substrate, patch morphology, and macrophyte species composition (Table S1) and included a macrophyte and gravel-bed plot. The lateral location of each plot (river right vs. left) was randomly assigned between pairs and plot sizes measured 1.5 m². For each paired plot, two patches of *Ranunculus aquatilis* (common water crowfoot) were chosen, and one was randomly selected for removal of emergent stems at the streambed surface. Upon removal of macrophytes, a localized disturbance (walk through) was implemented in each macrophyte plot to account for disturbance effects between plots. Due to the limited spatial extent of gravel-bed habitat, especially during the summer macrophyte growing season, gravels were augmented from a local source. Gravels were removed from the streambed downstream of the plots, dried for 36 hr, and placed within the macrophyte removal plot. Plots were allowed to incubate for five weeks before invertebrate seasonal sampling commenced (July 2008). Rebar was placed in the streambed to mark the most upstream corners of each plot, and a sample quadrat was used to randomly select seasonal samples within each patch. Rebar placement ensured that the same macrophyte and gravel patches were sampled during each period.

2.3 | Invertebrate sampling and stream velocity

To understand seasonal variability, benthic invertebrates were sampled from both macrophyte and gravel-bed plots with a modified Hess sampler (335- μ m mesh, 0.037-m² sample area) during three periods (July 2008, September 2008, and May 2009; Table S2). For study purposes, we refer to these periods as summer, fall, and spring, acknowledging that detailed invertebrate seasonal dynamics likely requires higher temporal resolution of sampling. Sample locations were randomly selected in each plot. All samples were placed in a bucket, elutriated, filtered through a 100- μ m mesh net, and preserved in 95% ethanol. For macrophyte plots, plants were removed to bed surface with scissors during invertebrate sampling. Macrophytes were then rinsed, and invertebrates were removed. Macrophytes were stored in separate plastic bags, placed in a cooler, and transported back to the laboratory for additional processing (see laboratory procedures).

Hydraulic monitoring was conducted during each sample period immediately downstream of macrophyte and gravel plots. During each sample period, point velocities were measured at two-tenths (near water surface), six-tenths (midwater column), and eight-tenths (immediately above streambed surface) water column depth using a Marsh–McBirney Flo-Mate electromagnetic velocity metre attached to a top-setting wading rod. Multiple depth measurements were selected in order to assess common juvenile salmonid feeding positions.

2.4 | Drift study

At the stream reach scale, we measured the relative contribution of macrophyte habitat to invertebrate drift. Eight distinct stream reaches were delineated for drift sampling (Figure 1). Each reach was selected

based on canopy cover, wetted width, water depth, and percentage of macrophyte cover (Table S3). Four of the stream reaches contained less than 5% cover of *R. aquatilis* (i.e., gravel-bed reach), whereas an additional four reaches contained greater than 75% cover *R. aquatilis* (i.e., macrophyte reach). Numerous studies have shown that invertebrate drift often exhibits diel periodicity with a large increase in drift coinciding with the hour after sunset (Brittain & Eikeland, 1988). Therefore, we conducted drift sampling using a complete random block design where we blocked for date, for 1 hr immediately after sunset on April 28 and 29, 2009.

For each replicate reach, two parallel drift nets were deployed (350- μ m mesh, 0.008-m² net opening). Immediately after sampling, a Marsh–McBirney Flo-Mate electromagnetic velocity metre was placed within the mouth opening of each net, and water velocity was recorded. Final velocities were calculated by averaging both velocity measurements in each reach. Sampling nets were removed from the river, and contents were composited into a bucket. Samples were elutriated and filtered through a 100- μ m mesh net, preserved in 95% ethanol in the field, and returned to the laboratory. Entire samples were counted, and aquatic invertebrates were identified to genus or the lowest practical taxonomic level. Drift was calculated as drift volume or the number of drifting aquatic organisms per cubic metre of water.

2.5 | Salmonid habitat usage

Snorkel surveys were conducted over 25 river reaches to assess juvenile salmonid habitat preference and utilization during 2008 (Figure 1). Surveys were conducted one to two times per month depending on hydrologic conditions. Due to the spring-fed nature of the stream, traditional geomorphic habitat (pool, riffle, run, etc.) criteria were not suitable. Instead, a site-specific habitat classification system was created to physically describe 100% of the wetted channel for each surveyed reach. Habitats included six types of channel margin and/or in-channel aquatic habitat, including point bars, active cut-banks, perennial and/or ephemeral backwaters, large woody debris, emergent vegetation, and aquatic macrophytes. For each reach, individual habitats (multiple habitats were present in individual reaches) were delineated on aerial photographs, and polygons were built in Geographic Information System (GIS) to quantify the aerial extent of each habitat type. Snorkel surveys were conducted in an upstream direction, and fish were only counted within 1 m of each side of the snorkeler and within the targeted habitat. During each survey, the snorkeler identified fish species and age class, and habitat occupied and recorded the information on a wrist slate.

2.6 | Laboratory processing

For the paired plot study, all plant samples were rerinsed in the laboratory within 48 hr, and the remaining invertebrates were removed. Each plant sample was examined under a dissecting microscope to ensure the removal of all invertebrates. Laboratory processed invertebrates were placed in sample containers, and macrophytes were subsequently dried at 65°C for 36 hr and weighed on an electronic balance (± 0.01 g). Dried macrophytes were ashed in a muffle furnace

at 475°C for 90 min or until the entire sample consisted of ash, cooled to room temperature, and weighed again. Macrophyte ash free dry mass (g) was calculated by subtracting the mass of inorganic residue from the precombustion dry mass.

Invertebrate samples for taxonomic determination were obtained by randomly subsampling, using a plankton splitter to reach a minimum count of 500 organisms. Most aquatic invertebrates were identified to genus when possible using Merritt, Cummins, and Berg (2008); Wiggins (1996); Smith (2001); and Thorp and Covich (2001) as well as various taxonomic-specific references. Ostracoda, Oligochaeta, and Arachnida were identified to class, whereas Chironomidae were identified to family. Specimens in poor condition or early instars were identified to the highest practical taxonomic level.

2.7 | Data analysis

Benthic invertebrate density (no. individuals·m⁻²) was calculated based on the fraction of each sample sorted and the area of streambed sampled. Both benthic and drift data were ln-transformed prior to analyses, and a Shapiro–Wilk test was used with habitat residuals to confirm normality. Homogeneity of variance across samples for each date was verified using a Levene test for homoscedasticity. Repeated measures analysis of variance (rmANOVA) was used to compare benthic invertebrate density through time for each habitat, with habitat (macrophyte and gravel) as the between subjects factor and date as the within subjects factor. Invertebrate drift density between habitats was analysed using a two-tailed *t* test. We addressed potential differences in water velocity between gravel and macrophyte plots by performing a series of stratified rmANOVAs at two-tenths, six-tenths, and eight-tenths water depth and conducted a Shapiro–Wilk test of normality with treatment residuals to ensure that data were normally distributed.

Differences in invertebrate community structure between habitats were analysed using nonmetric multidimensional scaling (NMDS). NMDS uses invertebrate presence and abundance data to depict community similarity in two-dimensional space. The spatial proximity of samples indicates a high degree of similarity of invertebrate community structure between habitats. We square-root transformed abundance data for each sample, and Sørensen distances were calculated to display community similarity between samples and sites. NMDS statistical analyses were conducted in *R* using the “vegan” (Oksanen et al., 2013), “betapart” (Baselga & Orme, 2012), and “ecodist” (Goslee & Urban, 2007) packages.

Invertebrate diversity was examined by calculating several metrics, including taxa richness, functional feeding group analysis, Shannon's diversity, and Simpson's reciprocal diversity. Both taxa richness and functional feeding group data were ln-transformed prior to statistical analysis to meet assumptions of normality. An rmANOVA was used to test for difference for each respective metric through time for each habitat, with habitat as the between subject factor and date as the within subject factor. The model assumptions were checked using a Shapiro–Wilk test of normality and a Levene test of homoscedasticity. We set our experiment-wise Type I error rate (α) at 0.05 and used Bonferroni–Holm (step down) adjusted *p* values when tests involved multiple comparisons as with individual taxon

density comparisons between habitats for the 28 most common taxa. We defined common as a taxon accounting for at least 0.1% of all invertebrates sampled during the study period. Except as mentioned above, all statistical analysis was performed using SAS version 9.2 or JMP version 8.0.

3 | RESULTS

3.1 | Invertebrate density and macrophyte biomass

We found highly significant differences in invertebrate density between habitat types (rmANOVA habitat $p < 0.0001$; Figure 2), with macrophytes supporting up to nine-fold greater invertebrate densities than gravel habitat. Overall, invertebrate densities peaked in July and were lower during spring and fall (rmANOVA date, $p < 0.0001$). Both macrophyte and gravel-bed habitat supported the greatest invertebrate densities during summer (139,802 and 42,111 individuals·m⁻², respectively), whereas gravels exhibited their lowest densities during spring (15,352 individuals·m⁻²) and macrophytes during fall (84,619 individuals·m⁻²). Plant biomass declined throughout the study period and decreased by nearly a factor of two between spring and fall (rmANOVA $p < 0.001$). We also found a strong correlation between macrophyte biomass and invertebrate density ($r^2 = 0.54$, $p = 0.002$; Figure 3).

3.2 | Invertebrate diversity and community composition

Gravel-bed habitat supported a more diverse invertebrate assemblage than macrophyte habitat. Invertebrate taxa richness associated with gravel-bed habitat was significantly greater than macrophyte habitat, and Shannon–Wiener and Simpson's reciprocal diversity followed a similar pattern (Table 1). Taxa richness was also greater during the summer and fall than spring for both macrophyte and gravel-bed plots (rmANOVA date, $p < 0.05$), but seasonal differences in Shannon or Simpson's diversity were not detected.

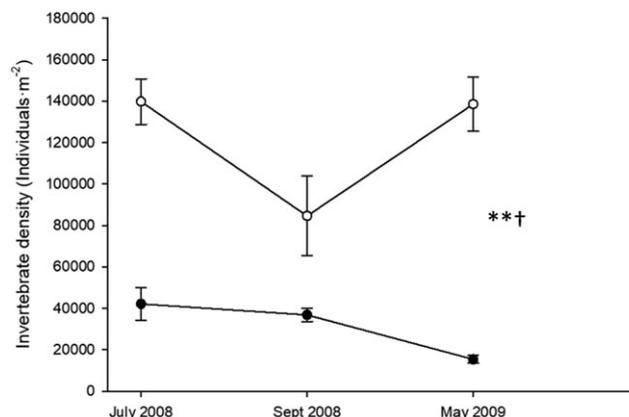


FIGURE 2 Number of individuals·m⁻² on gravel and macrophyte plots (± 1 standard error, SE) during the summer and fall of 2008 and spring of 2009: open circles, macrophytes; solid circles, gravel. **, A significant difference in invertebrate density between gravel and macrophyte plots ($p < 0.001$); †, a significant difference between date ($p < 0.05$)

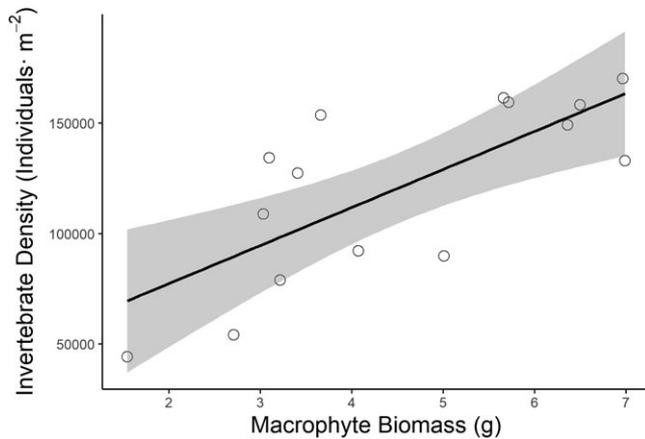


FIGURE 3 Linear regression of invertebrate density (individuals·m⁻²) and plant biomass for all macrophyte plots ($n = 15$) during the study period ($r^2 = 0.54$, $p < 0.01$). Shaded region is the 95% confidence interval of mean predictions

We found strong differences in functional feeding guilds between macrophyte and gravel habitat. Macrophyte plots showed a greater contribution of both collector gatherers and collector filterers to assemblage patterns than gravel plots ($p < 0.0001$; Figure 4). Over all seasons, collector gatherers accounted for 80% of the total macrophyte assemblage and collector filterers accounted for an additional 10%. Invertebrate assemblages on macrophytes were generally dominated by *Baetis*, *Hyallela*, ostracods, and Chironomidae. Analysis also indicated that collector gatherers and collector filterers were abundant during spring and summer and declined during fall (rmANOVA date, $p < 0.05$).

Grazing invertebrates showed a strong preference for gravel habitat (rmANOVA, $p < 0.0001$; Figure 4). Grazers were most dominant during fall, accounting for 45% of the entire gravel invertebrate assemblage, but only 5% of the macrophyte invertebrate assemblage during the same period. During this time, *Optioservus* and *Rhithrogena* accounted for up to 33% of the gravel invertebrate community and were the dominant grazers throughout the study period, regardless of season. We found no seasonally significant differences in grazer contribution for either habitat between dates and no significant differences in the contribution of predator or shredder functional groups between habitats. There were, however, more predators during spring and fall than summer (rmANOVA date, $p < 0.05$).

Invertebrate community composition varied strongly with habitat type, showing clear spatial distinction between gravel and macrophytes along Axis 1. Nonmetric multidimensional ordination scaling

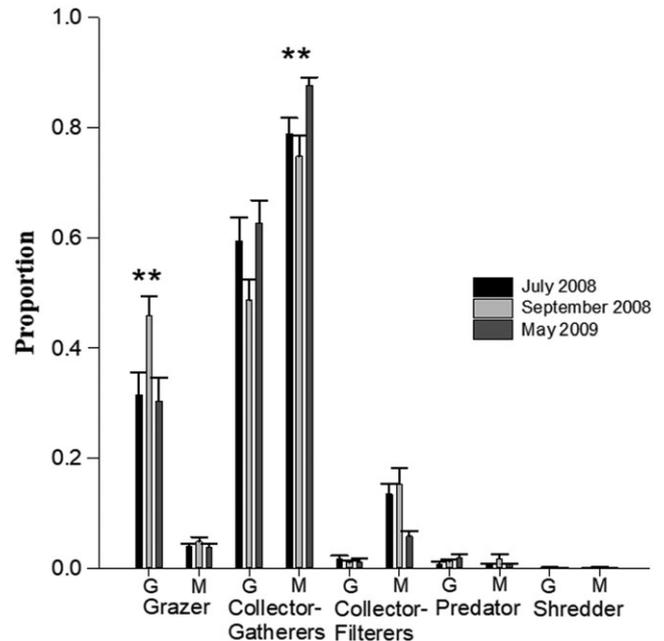


FIGURE 4 Mean relative abundance of functional feeding groups by season and habitat type (G: gravel; M: macrophyte). **, A significant difference in a group between gravel and macrophyte plots ($p < 0.001$)

indicated that communities were spatially distinct with a stable two-dimensional solution (stress = 0.12, cumulative $R^2 = 0.98$; Figure 5), based on the 28 most common invertebrate taxa sampled. Macrophyte samples exhibited a tighter spatial clustering than gravel samples throughout the study period, reflecting less variability in community composition between seasons.

3.3 | Individual taxon densities

Individual taxon densities varied sharply depending on habitat type (Table 2). Macrophytes were shown to support higher densities of *Hyallela*, *Simulium*, *Baetis*, *Dipheter*, *Brachycentrus*, *Juga*, and oligochaetes (rmANOVA, $p < 0.0018$; Table 2), after Bonferroni corrections for statistical significance ($0.05/28 = 0.0018$ for the 28 most common taxa evaluated). Conversely, gravels supported higher densities of *Optioservus* (larvae), *Rhithrogena*, *Protoptila*, and *Physa* (rmANOVA, $p < 0.0016$; Table 2). Most of these differences reflected greater abundance in macrophyte habitat (Table 2). In general, macrophyte and gravel-bed habitat supported distinct assemblages throughout the study period.

TABLE 1 Taxa richness, Shannon–Wiener diversity, and Simpson's reciprocal diversity compared between gravel and macrophyte plots over three seasons

Date	Taxon Richness		Shannon's Diversity		Simpson's Reciprocal Diversity	
	Gravel ^{*,†}	Macrophyte	Gravel*	Macrophyte	Gravel*	Macrophyte
July 2008	24.8	23.6	2.4	2.1	8.1	5.9
Sept. 2008	27.0	23.0	2.3	2.2	6.3	6.3
May 2009	21.6	19.2	2.3	1.8	7.7	3.9

*A significant difference in invertebrate density between gravel and macrophyte plots.

†A significant difference between date; $p < 0.05$.

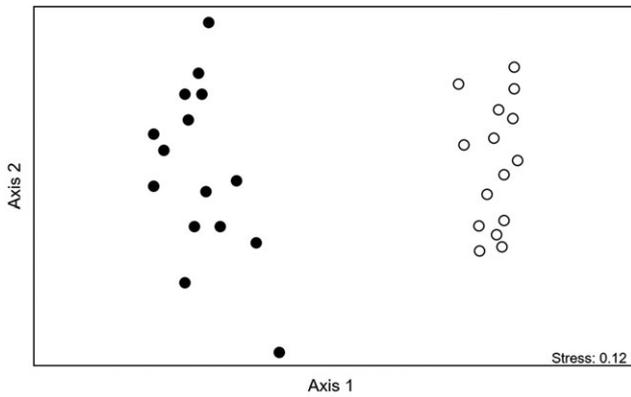


FIGURE 5 Nonmetric multidimensional scaling ordination results based on mean densities of invertebrates for gravel and macrophyte plots over all seasons ($n = 15$). Gravel samples (black circles) are clearly separated from macrophyte samples (white circles) indicating distinct assemblage patterns

3.4 | Water velocity and drift

Water velocity was reduced by up to 42 times behind macrophyte plots when compared with gravel plots (six-tenths depth, May 2009). Over all seasons, average velocities declined by 1.5, 35, and 15 times behind macrophyte plots as compared with gravel plots at two-, sixth-, and eighth-tenths depth, respectively. There were no significant differences in water velocity between macrophyte and gravel plots at two-tenths depth ($p = 0.07$), but strong statistical differences at sixth- and eighth-tenths depth ($p < 0.0001$; Table 3).

Invertebrate drift was 2.3 times greater in macrophyte reaches than gravel-bed reaches (t test, $p < 0.05$; Figure 6). Regardless of reach type, *Dipetor hageni*, *Baetis*, and *Hyallela* accounted for over 60% of the total invertebrate drift assemblage. Ostracods accounted for another 14% of drift in macrophyte reaches, while *Brachycentrus*, a collector-gathering trichopteran, comprised an additional 13% of drift in gravel-bed reaches.

TABLE 2 Comparison of individual taxon densities (no. individuals·m⁻²) between gravel and macrophyte plots

Taxon	FFG	Gravel		Macrophyte		rmANOVA	
		Mean ± SE	Density	Mean ± SE	Density	F	p
Baetis*	CG	61	17	844	147	207.33	<0.0001
Dipetor*	CG	35	6	179	24	41.09	<0.0002
Ephemera	CG	14	5	19	4	4.56	0.0652
Paraleptophlebia	CG	4	1	33	10	6.85	0.0308
Rhithrogena*	SC	89	15	1	0	477.72	<0.0001
Tricorythodes	CG	42	13	27	22	7.62	0.0247
Amiocentrus	CG	7	3	2	1	2.73	0.1371
Brachycentrus*	CG	1	1	60	18	44.54	<0.0017
Hydropsyche	CF	5	2	8	3	0.44	0.5263
Hydroptila	PH	10	6	0	0	12.80	0.0072
Protophila (L)*	SC	38	11	2	1	55.21	<0.0001
Protophila (P)	—	6	3	0	0	11.69	0.0091
Chironomidae	Various	106	21	244	48	16.15	0.0039
Simulium*	CF	2	1	169	48	53.07	<0.0001
Acari	P	17	5	10	2	3.79	0.0874
Optioservus (L)*	SC	153	31	15	6	51.49	<0.0001
Optioservus (A)	SC	24	6	5	3	13.83	0.0059
Coenagrionidae	P	4	1	27	8	10.34	0.0123
Glossiphoniidae	PA	2	1	3	1	0.01	0.9123
Juga*	SC	30	6	106	19	25.77	<0.001
Physa*	SC	3	1	23	5	23.74	<0.0012
Vorticifex	SC	21	7	7	2	0.68	0.4338
Sphaeriidae*	CG	5	2	175	36	105.90	<0.0001
Hyallela*	CG	214	72	1231	222	33.61	<0.0004
Hydra	—	0	0	41	16	12.86	0.0071
Oligochaeta*	CG	62	11	264	45	28.17	<0.0007
Ostracoda	CG	33	17	363	102	12.71	0.0073
Platyhelminthes	—	6	2	27	6	8.30	0.0205

*A significant difference after Bonferroni–Holm corrections for statistical significance, $0.05/28 = p < 0.0018$.

TABLE 3 Water velocity (m/s) at common salmonid drift feeding positions immediately downstream of gravel and macrophyte plots

Date	20% Depth		60% Depth		80% Depth	
	Gravel	Macrophyte	Gravel	Macrophyte**	Gravel	Macrophyte**
July 2008	0.48	0.32	0.33	0.02	0.20	-0.01
Sept. 2008	0.42	0.32	0.34	0.04	0.22	0.01
May 2009	0.92	0.63	0.73	-0.02	0.51	-0.07

**A significant difference in water velocity between gravel and macrophyte plots; repeated measures analysis of variance, $p < 0.0001$.

3.5 | Salmonid habitat usage

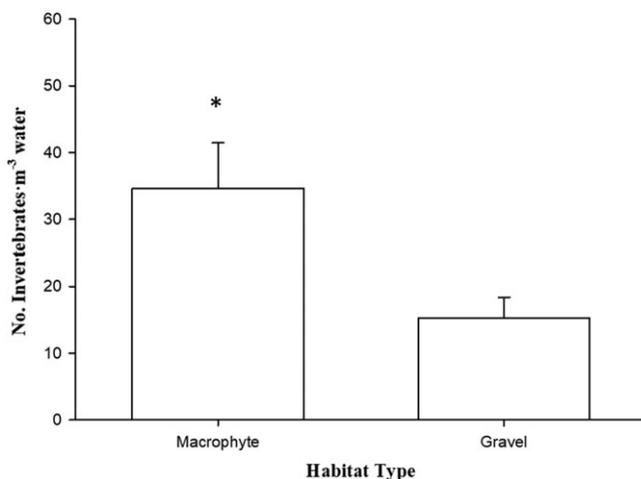
A total of 132 snorkel surveys were conducted during 2008. During those surveys, 474 young of the year (YOY) steelhead were observed while 55 aged 1+ steelhead were observed. Juvenile steelhead preferentially selected macrophyte habitat at a rate 3.2 times greater, on average, than the five other habitat types. Overall, macrophyte habitat accounted for approximately 40% of all YOY steelhead observed (Figure 7).

4 | DISCUSSION

We found strong differences in juvenile salmonid habitat selection, invertebrate prey density and drift, and hydraulic character between macrophyte and gravel-bed habitat. We also found that different habitat types supported distinct invertebrate communities. While abiotic factors, such as thermal and flow regimes, are often cited as enhancing fish populations in spring-fed rivers (NRC, 2004), this study shows that primary producers (aquatic macrophytes) can strongly influence food web dynamics and represent important rearing habitat for higher order consumers, such as juvenile salmonids. We suggest that macrophytes were likely a major reason why this and similar spring-fed rivers (see Lusardi et al., 2016) function as high-quality rearing habitats for salmonids.

4.1 | Invertebrate abundance and diversity

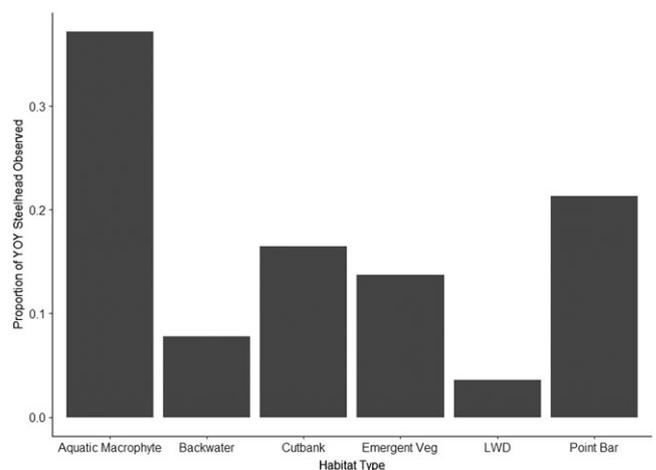
Our results show that macrophyte habitat supported a greater density of invertebrates than gravel-bed habitat throughout the study period,

**FIGURE 6** Number of drifting invertebrates per cubic metre of water (± 1 standard error, SE; $p < 0.05$)

providing additional prey for foraging fishes. On average, invertebrate density in macrophyte habitat was nearly four times greater than in gravel-bed habitat and up to nine times greater during spring than fall, a critical time for salmonid rearing. Both habitats showed peak invertebrate densities during summer, suggesting maximization of primary productivity, available habitat, and invertebrate generation time during the period (Strayer & Malcom, 2007; Wright, 1992). In contrast, the lowest invertebrate density in gravel habitat occurred during spring, which was likely due to limited epilithic algae recruitment, winter scour, and life history timing of certain grazing invertebrates. Macrophyte invertebrate densities showed strong declines during fall, the likely result of an overall reduction in habitat complexity or shift in macrophyte species composition (Table S4).

Overall, strong differences in invertebrate density between the two habitats were likely related to the relative increase in habitat complexity and available surface area provided by macrophytes (Taniguchi et al., 2003). Additional benefits for invertebrates associated with macrophyte habitat include reductions in water velocity within stands (Cotton et al., 2006; Wharton et al., 2006), refuge from predators (Beckett, Aartila, & Miller, 1992), and the availability of diverse food resources such as epiphytic algae, detritus, and fine particulate organic matter (Carpenter & Lodge, 1986; Gregg & Rose, 1982; Koetsier & McArthur, 2000). Although a combination of these factors likely explains the large differences in invertebrate density between macrophyte and gravel habitat, plant density may be the primary determinant.

We showed a strong positive correlation between macrophyte biomass and invertebrate density, similar to previous studies (Crowder & Cooper, 1982; Heck & Wetstone, 1977). Strayer and Malcom (2007)

**FIGURE 7** Observed juvenile steelhead habitat utilization between six habitat types. LWD: large woody debris

attributed this correlation to a higher primary productivity, increased colonization space for both invertebrates and epiphytic algae, and increased refuge from fish predation. On the Shasta River, macrophyte plots exhibited their greatest biomass during summer, a period of high light incidence, and experienced precipitous declines during fall. The epiphytic invertebrate assemblage followed a similar pattern, with density peaks during spring and summer and extensive declines during fall. During the fall sampling period, plant biomass was reduced by nearly half and was associated with a similar decline in invertebrate density (40% decline between the summer and fall). Declines in individual taxa between summer and fall were most pronounced in *Baetis* (49% reduction), Chironomidae (33%), and *Hyallolella* (34%).

Contrary to our expectations, gravel habitat supported a greater diversity of invertebrates than macrophyte habitat, and functional feeding group analysis indicated that taxa were utilizing different resources between habitats. Although a few studies have found that gravel habitat supported a higher diversity of invertebrates than macrophytes (Alonso & Camargo, 2010; Coggerino, Cellot, & Bournaud, 1995), most have concluded the opposite. Shupryt and Stelzer (2009) found that macrophyte habitat supported a greater diversity of invertebrates than sand/gravel habitat due to enhanced habitat diversity and considered macrophyte beds as biological "hot spots." Similarly, Strayer and Malcom (2007) demonstrated that macrophytes were an important source of biodiversity when compared with unvegetated substrate in the Hudson River estuary. The differences between these studies are likely attributed to relative habitat availability between study systems, with rare habitats (either macrophytes or gravel) representing important contributors to invertebrate reach scale beta diversity.

Whereas macrophyte and gravel habitats both supported the dominant collector gatherer and filterer invertebrate guilds, grazers were almost exclusively associated with gravel habitat. At times, grazers accounted for up to 45% of the entire gravel habitat invertebrate assemblage (July 2008), while never accounting for more than 5% of the macrophyte assemblage (September 2008). This suggests that genera such as *Rhithrogena* and larval *Optioservus*, two numerically dominant grazers throughout the study period, depend on epilithic algal production and other microhabitat features associated with gravel habitat. Thus, while both habitats supported genera from collector-gatherer and -filterer functional guilds, gravel habitat also supported numerous grazing invertebrates. These rare grazing invertebrates accounted for differences in species diversity between habitats. Such differences have important implications for reach-scale beta diversity and conservation. For instance, Astorga et al. (2014) found that habitat diversity was a primary driver of stream invertebrate beta-diversity in numerous rivers in New Zealand, and others have come to similar conclusions using various study organisms (Hewitt, Thrush, Halliday, & Duffy, 2005; Veech & Crist, 2007).

In the western United States, stream ecosystems are changing at an alarming rate due to climate change and other anthropogenic impacts, and species pools are becoming more homogenized as the persistence of rare species becomes less likely (Durance & Ormerod, 2007; Moyle et al., 2017; Muhlfeld et al., 2011). In this study, rare habitat features may represent important secondary production diversity contributors that support stream ecosystem function and

stability despite their relative rarity. In turn, conservation of such habitats may promote ecosystem resilience in the face of a rapidly changing climate.

4.2 | Invertebrate drift and water velocity

We found strong differences in invertebrate drift between macrophyte and gravel dominated stream reaches. Muller (1954) and Waters (1961) suggested that invertebrate drift is a function of excess carrying capacity, serving to regulate population density. Our data suggest a strong positive relationship between invertebrate benthic density and drift between habitats. This ultimately facilitates foraging opportunities for salmonids and other stream dwelling fish that rely on drifting invertebrates as food resources.

Some have argued that invertebrate drift is controlled by top down and bottom up processes (Bohle, 1978; Flecker, 1992; Hildebrand, 1974; Peckarsky, 1980). However, we found no significant differences in invertebrate predator density between habitats and are unaware of a potential resource gradient between study reaches. Instead, we postulate that higher drift rates associated with macrophyte habitat was likely due to amplified intraspecific competition and/or interference competition associated with greater benthic standing crops of invertebrates in macrophytes plots than gravel plots (Walton, Reice, & Andrews, 1977). This becomes more evident when one considers that *Baetis* and *Hyallolella* were the dominant genera in both macrophyte drift (70%) and benthic macrophyte (65%) samples. Irrespective of the mechanisms contributing to higher drift rates in macrophyte reaches, our data support the notion that macrophytes are a highly productive habitat for both benthically foraging and drift feeding fishes.

Macrophyte beds are known to reduce water velocity and increase water depth and cross-sectional area (Champion & Tanner, 2000; Cotton et al., 2006; Sand-Jensen, 1998). Perhaps more importantly, and, from an ecological perspective, macrophytes provide velocity heterogeneity and refuges for certain organisms (Dodds & Biggs, 2002; Gregg & Rose, 1985; Sand-Jensen & Madsen, 1989). Less is known, however, about water velocity immediately downstream from macrophyte patches at common salmonid feeding positions. Direct seasonal comparisons between macrophyte and gravel plots yielded lower water velocity in all parts of the water column, although the differences in near-surface velocities were nonsignificant (two-tenths depth). Water velocity has been shown to strongly affect juvenile salmonid habitat selection (Morantz, Sweeney, Shirvell, & Longard, 1987). Our data therefore suggest that salmonids gain an energetic benefit by residing immediately downstream of macrophyte patches due to a combination of reduced water velocity and increased food resources. This view is consistent with Everest and Chapman (1972), who suggested that salmonids preferentially select habitats that reduce energy costs and maximize invertebrate drift availability. Similarly, Fausch and White (1981), among others (e.g., Fausch, 1984), affirmed that optimal stream positions for salmonids are those that minimize energy expenditure and maximize access to invertebrate drift, and that salmonid net energy gain should be most profitable in areas of high drift and low current velocities.

4.3 | Implications for rearing salmonids

The Shasta River historically accounted for more than half the entire Klamath Chinook salmon (*O. tshawytscha*) run, despite contributing approximately 2% of the annual discharge of the lower river basin (NRC, 2004; Wales, 1951). Although abiotic factors such as optimal flow and thermal regimes and geologically derived nutrients are cited as the foremost reasons for favourable salmonid growing conditions on the Shasta River (NRC, 2004), this study indicates that macrophytes are bioenergetically favourable habitat for dense populations of juvenile salmon and steelhead. YOY steelhead strongly preferred macrophyte habitat compared with other habitat types during 2008. Similar observations of juvenile steelhead utilizing macrophytes as habitat have also been described for Big Springs Creek in Idaho, a tributary to the Lemhi River (Chapman, 1966). Beland, Trial, and Kocik (2004) examined Atlantic salmon habitat preference on the Narragausus River in north-eastern Maine and found that juvenile salmonids preferred intermediate densities of macrophytes and suggested that this may be a response to prey availability. In a riparian canopy removal experiment, Riley et al. (2009) found that salmonids were more numerous and larger in open canopy reaches and attributed these responses to macrophyte growth and associated increases in secondary production. This research builds on previous studies by elucidating the mechanisms that confer rearing advantages to salmonids through aquatic macrophyte habitat selection. Such advantages may have important implications for growth and fitness of anadromous salmonids.

Restoration efforts focused on Pacific salmonid recovery in the Klamath River basin often target the Shasta River because of its unique hydrological and geological attributes, which can provide a stable flow regime and optimal thermal habitat for fish. We postulate that aquatic macrophytes represent an undervalued ecological condition of spring-fed systems that has the potential to enhance growth rates of juvenile salmonids when compared with other habitat types. Fully defining the benefits accrued through positive interactions between macrophytes and rearing salmonids is therefore important for determining restoration actions for salmonid conservation in spring-fed systems or any stream supporting large macrophyte beds.

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